

**THE ECOLOGY AND CONSERVATION OF
THE WHITE-WINGED NIGHTJAR
*CAPRIMULGUS CANDICANS***

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**A thesis submitted to the University of Cambridge in
candidacy for the degree of Doctor of Philosophy**

For my grandparents

DECLARATION

This thesis is the result of my own work, and includes nothing that is the outcome of work done in collaboration, except where specifically indicated in the text. The text does not exceed 80,000 words, and no part has been submitted to any other university in application for a higher degree or diploma.

Robert Pople

SUMMARY

In the tradition of previous studies of threatened species, this thesis was undertaken with the aim of improving our understanding of the ecology of the White-winged Nightjar *Caprimulgus candicans*, and providing the information necessary to facilitate conservation efforts on its behalf. In 1998-2001, I studied a population of White-winged Nightjars at Aguará Ñu, an area of cerrado habitats within the Reserva Natural del Bosque Mbaracayú, eastern Paraguay. Over the course of three fieldwork seasons, I captured and ringed a total of 49 nightjars (34 adults and 15 young birds). Young females first bred at approximately one year old, while still in pre-definitive plumage. Young males exhibited a form of delayed plumage maturation, whereby they only attained definitive plumage following a prolonged moult spanning much of their first potential breeding season. No evidence was obtained to suggest that they succeeded in breeding while in this conspicuously intermediate state of moult. Considerable variation was noted in the plumage whiteness of definitive males, but no clear evidence was found for consistent age-related increases in white. During the breeding season, males defended small aggregated display territories, at which they conducted nuptial display flights between late August and early January. Female nightjars were responsible for all the parental care, and apparently visited male display arenas solely to obtain copulations. Chick paternity data confirmed that the study population was polygynous, with patterns of male aggregation suggestive of an exploded lek or 'landmark' mating system. Radio-telemetry studies showed that nightjars utilised home ranges of at least 20 to 40 hectares during the eight to ten months for which they were monitored. Home ranges contained a disproportionately large amount of young campo cerrado vegetation, but no forest or old campo cerrado habitats. When selecting foraging sites within their ranges, nightjars preferred younger and avoided older campo cerrado vegetation; wet grassland was utilised roughly in proportion to its availability. Observed patterns of habitat selection were potentially explained by the greater abundance of insect prey in younger habitats. When selecting daytime roost sites, nightjars preferred vegetation of intermediate age, reflecting their need for a balance between cover and ease of access. A more general analysis of patterns of sexual dimorphism within the Caprimulgidae showed that, although almost 80% of nightjar species exhibit some dimorphism of plumage whiteness, the study species was by far the most extreme case. The striking plumage of the male was partly explained by a strong positive relationship between wing white and openness of breeding habitats within the family. However, this failed to explain the complete absence of white in the female plumage, or the extent of white dimorphism shown by the species. The most likely explanation would appear to be that extreme plumage dimorphism occurred in conjunction with the evolution of polygyny and female-only care in this open-country species. The implications of these findings for the conservation of the White-winged Nightjar are highlighted, and recommendations are proposed for future work and conservation action.

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CHAPTER 1

INTRODUCTION

“The song of the Dodo, if it had one, is forever unknowable because no human from whom we have testimony ever took the trouble to sit in the Mauritian forest and listen.”

David Quammen, *The Song of the Dodo* (1996)

CONSERVING BIRD BIODIVERSITY

Reports of an ungainly, flightless pigeon-like bird, nicknamed “walckvögel” or “disgusting bird” by Dutch sailors, first reached Europe around 1600. The last credible account of a live individual dates from 1662. In the interim, the species was hunted mercilessly, and its nests and young were depredated by the pigs and monkeys introduced by humans to its native island of Mauritius. By 1690, if not earlier, the species was extinct. The story of this tragicomic bird, better known as the Dodo *Raphus cucullatus*, is one of the best known examples of human-caused extinction. Sadly, it was not an isolated case. In total, 128 species of bird are believed to have gone extinct during the last 500 years, 103 of these since 1800 (Norris & Pain 2002), and a further 1,186 species are currently threatened with global extinction (BirdLife International 2000). The rate at which bird species are being lost is currently greater than at any other time in the group’s evolutionary history (Smith *et al.* 1993, Pimm *et al.* 1995). Some species, like the ill-fated Dodo, are almost certainly being lost before their habits, and possibly even their existence, can be documented.

Birds are potentially useful indicators of global biodiversity, as they have dispersed to, and diversified in, virtually all terrestrial regions, habitats and altitudes of the world (ICBP 1992, BirdLife International 2000). That they are currently faced with widespread decline around the globe is symptomatic of the underlying malaise affecting the way we treat our planet (Bibby 2002). The study of birds is hence not solely an esoteric pastime for a comfortable few, but rather a means of addressing the problems that humans continue to cause as a result of their unsustainable use of the world’s resources. The primary objective of conservation is the prevention of local and global extinctions, through the diagnosis and treatment of population declines (Caughley 1994, Green 2002). By their very nature, however, many threatened species are extremely poorly known, limiting the effectiveness of conservation efforts on their behalf. A recent overview of the status of the world’s birds indicates that 44% of threatened species still need urgent research on their ecology, and 21% on the nature and causes of the threats facing them, before effective conservation action can be undertaken (BirdLife International 2000).

BIRD CONSERVATION IN THE NEOTROPICS

The ancient origins of South America, and its complex topography and climate, have led to a mosaic of varied habitats and a spectacular diversity of plant and animal species. The Neotropics, or New World tropics, are particularly speciose, supporting 3,800 (40%) of the world's bird species in just 16% of its land area (Collar *et al.* 1997). This diversity is also apparent at higher taxonomic levels, with 90 of the world's 150 bird families occurring in the Neotropics, and 28 of these endemic to the realm (Stotz *et al.* 1996). However, a long history of human colonisation, and the various economic, social and political factors associated with this, have led to serious changes to the region's ecosystems. Many of the great forests are being felled, the natural grasslands cultivated and the wetlands drained. Inevitably, these disturbances have had grave consequences for the region's avifauna, with 324 (9%) Neotropical bird species currently considered at risk of extinction, over 76% of these due primarily to the destruction and alteration of their habitats (Collar *et al.* 1997).

Although the majority of globally threatened birds are dependent on forest, almost 12% of Neotropical species are confined to grasslands – over twice as many as any other non-forest habitat (Wege & Long 1995). Nevertheless, the destruction of open country habitats continues to be greatly overshadowed by deforestation as a conservation issue (Collar 1996, Parker & Willis 1997), in no small part because the transformation of grassland landscapes is less spectacular than forest clearance (Bucher & Nores 1988). Recently, however, the main grassland-based ecoregions of central South America – the Mesopotamian grasslands of north-east Argentina, and the Cerrado – have increasingly become recognised as among the highest conservation priorities in the Neotropics (Dinerstein *et al.* 1995, Collar 1996, Stotz *et al.* 1996).

THE PLIGHT OF THE CERRADO

The Cerrado is the second largest biome in South America, covering an area of 1.5-1.8 million km² in central Brazil and, to a lesser extent, eastern Bolivia and north-eastern Paraguay (Ab'Saber 1977, 1983). It occupies a central position within the continent, separating the two large forest biomes of Amazonia and the Atlantic Forest, and bordering the open habitats of the Caatinga and the Chaco, to the north-east and south-west respectively (Cavalcanti 1988, Silva 1997). The region supports a variety of vegetation types, including wetlands, gallery forests and tropical dry forests, but the majority of its area is dominated by a savanna-like vegetation known as 'cerrado' (Eiten 1972). Cerrado *sensu lato* includes a natural gradient of physiognomies, varying with local soil properties and the range of human disturbance, e.g. wood-cutting, grazing and fires (Pivello & Coutinho 1996). These physiognomies range from open grasslands ('campo limpo'), through intermediate savanna forms with increasing woody vegetation ('campo sujo', 'campo cerrado' and 'cerrado' *sensu stricto*), to sclerophyllous forests or 'cerradão' (Eiten 1972, Coutinho 1982).

Until the middle of the last century, the Cerrado remained sparsely populated, and was effectively protected from human exploitation by its remoteness, and the acidity and aluminium toxicity of its soils. Since the 1950s, however, human disturbance has increased considerably, as a result of the construction of major highways, and generous state subsidies and tax incentives encouraging agricultural development (Ratter *et al.* 1997, Cavalcanti 1999). The region's deep soils and rolling terrain are well suited to mechanised agriculture, and the advent of liming and fertilisers opened the way for large-scale cultivation of cash crops, such as rice and soybean (Cavalcanti 1988, Ratter *et al.* 1997). The consequences were disastrous: more than 35% of the Cerrado had been converted to arable land, pasture or altered fallow by 1994 (Ratter *et al.* 1997), with other assessments suggesting that as much as 67% of the region has been "heavily or moderately altered" by human activities (Conservation International 1999). The scale of this devastation prompted Collar *et al.* (1992) to describe the situation as "one of the greatest ecological disasters in South America".

Sadly, the plight of the Cerrado has not been helped by the paucity of protected areas in the region. Fewer than 100 national parks or ecological reserves exist in the Cerrado, protecting just 32,000 km², or 1.5% of its total surface area (Ratter *et al.* 1997, Cavalcanti 1999). The majority of protected areas are less than 25,000 ha in size, and large subregions of the Cerrado – such as the newly created state of Tocantins in Brazil – have only one or two reserves (Cavalcanti 1999). Moreover, the conservation of existing reserves is increasingly complicated by two widespread, and largely intractable, management problems: wildfires (Pivello & Coutinho 1996, Pivello & Norton 1996, Silveira *et al.* 1999) and invasion by alien grass species (Pivello *et al.* 1999a,b). In recognition of the limitations of the current protected area system, a major priority-setting exercise recently identified urgent priorities for biodiversity conservation in the Cerrado, including the consolidation of existing protected areas, the co-ordination of faunal and floral inventories, and the creation of new conservation areas (Conservation International 1999).

STATUS OF THE CERRADO AVIFAUNA

The Cerrado supports a very diverse avifauna, with 759 bird species from 63 families known or assumed to breed in the region. This high species richness is due in part to the considerable environmental heterogeneity apparent within the region: while 52% of the Cerrado's birds depend on forests, 27% are dependent on open habitats, and 21% use both open and forested habitats (Silva 1995). Twenty-nine (4%) breeding species are endemic to the region (Silva 1995, 1997), including 16 (55%) that depend on its open country habitats (i.e. campo grasslands, cerrado *sensu stricto* and montane scrub, or 'campos rupestres', of the high plateaus). Given the wholesale devastation of Cerrado habitats (see earlier), it is unsurprising that 18 (64%) regional endemics were listed as globally threatened or near threatened when the current study began (Collar *et al.* 1994; Table 1.1).

Table 1.1 Threat status, sensitivity to disturbance, research priority and preferred habitat of 29 species of bird endemic to the Cerrado region (*per* Silva 1995, 1997).

Species	Threat status [†]	Sensitivity [‡]	Research priority [‡]	Primary habitat [‡]
Lesser Nothura <i>Nothura minor</i>	VU	High	High	Campo grasslands
Dwarf Tinamou <i>Taoniscus nanus</i>	VU	High	High	Campo grasslands
Chestnut-bellied Guan <i>Penelope ochrogaster</i>	VU	High	High	Gallery forest
Blue-eyed Ground-dove <i>Columbina cyanopis</i>	CR	High	High	Campo grasslands
Maroon-faced Parakeet <i>Pyrrhura pfrimeri</i> ¹		High	Medium	Deciduous forest
Yellow-faced Amazon <i>Amazona xanthops</i>	VU	Medium	High	Cerrado
White-winged Nightjar <i>Caprimulgus candicans</i>	CR	High	High	Campo grasslands
Hyacinth Visorbearer <i>Augastes scutatus</i>	NT	Medium	Medium	Montane scrub
Campo Miner <i>Geobates poecliopterus</i>	NT	Medium	High	Campo grasslands
White-lored Spinetail <i>Synallaxis albilora</i> ²		Low	Low	Gallery forest
Cipó Canastero <i>Asthenes luizae</i>	EN	Medium	High	Montane scrub
Planalto Foliage-gleaner <i>Philydor dimidiatus</i>	NT	High	Medium	Gallery forest
Henna-capped Foliage-gleaner <i>Hylocryptus rectirostris</i> ³	NT	High	Medium	Gallery forest
Large-billed Antwren <i>Herpsilochmus longirostris</i>		Medium	Medium	Gallery forest
Bananal Antbird <i>Cercomacra ferdinandi</i>		Medium	Medium	River-edge forest
Collared Crescentchest <i>Melanopareia torquata</i>		Medium	Medium	Cerrado
White-breasted Tapaculo <i>Scytalopus novacapitalis</i>	VU	High	High	Gallery forest
Reiser's Tyrannulet <i>Phyllomias reiseri</i>	NT	Medium	Medium	Deciduous forest
Grey-backed Tachuri <i>Polystictus superciliaris</i>	NT	Medium	Medium	Montane scrub
Caatinga Black-Tyrant <i>Knipolegus franciscanus</i>		Medium	Medium	Deciduous forest
Helmeted Manakin <i>Antilophia galeata</i>		Medium	Low	Gallery forest
Cinereous Warbling-finch <i>Poospiza cinerea</i>	NT	High	High	Campo grasslands
Pale-throated Pampa-finch <i>Embernagra longicauda</i>	NT	Medium	High	Montane scrub
Coal-crested Finch <i>Charitospiza eucosma</i>	NT	High	High	Cerrado
Crimson-fronted Cardinal <i>Paroaria baeri</i>		Medium	Medium	Riparian thickets
Black-throated Saltator <i>Saltator atricollis</i>		Medium	Medium	Cerrado
Blue Finch <i>Porphyrospiza caerulescens</i> ⁴	NT	Medium	High	Campo grasslands
White-striped Warbler <i>Basileuterus leucophrys</i>		Medium	Medium	Gallery forest
Curl-crested Jay <i>Cyanocorax cristatellus</i>		Medium	Medium	Cerrado

Taxonomic notes: ¹ treated as a subspecies of *Pyrrhura leucotis* by Parker *et al.* (1996); ² *Synallaxis simoni* in Silva (1997), but subsumed within *S. albilora* by Parker *et al.* (1996); ³ *Automolus rectirostris* in Silva (1997); ⁴ *Passerina caerulescens* in Silva (1997).

[†] CR = Critical; EN = Endangered; VU = Vulnerable; NT = Near Threatened (from Collar *et al.* 1994).

[‡] Data from Parker *et al.* (1996); 'Primary habitat' taken as first habitat category listed for each species.

Many Cerrado species are highly sensitive to disturbance from grazing, wildfires and the invasion of alien grass species (e.g. Teixeira & Negret 1984, Cavalcanti 1988, Cavalcanti & Alves 1997, Cavalcanti 1999, Tubelis & Cavalcanti 2000), and nearly all endemic or near-endemic species have suffered drastic declines as a result of recent human activities (Collar *et al.* 1997, Parker & Willis 1997). Nevertheless, the ecology and conservation requirements of many endemics remain extremely poorly known, and for some even basic information about their natural history is lacking (Silva 1999). Further evidence of this is provided by a search of the ISI Web of Science bibliographic database (Expanded Science Citation Index). Although this database does not cover certain regional ornithological journals (e.g. *Ararajuba*, *Cotinga*, *Ornitologia Neotropical*), it does include the majority of those in which most ornithological research has been published since 1981. Titles, abstracts and key words were searched for all variations of the common and scientific names of each of the 29 Cerrado endemics, but just nine articles were found, and five of these were about species considered ‘of least concern’ by Collar *et al.* (1994).

This dearth of knowledge is particularly acute for open country species, which constitute 11 of 13 Cerrado endemics rated as being of ‘high’ research priority by Parker *et al.* (1996; Table 1.1). Recently, a small number of studies have investigated the effects of disturbance and habitat degradation on populations of Cerrado birds (e.g. Cavalcanti & Alves 1997, Tubelis & Cavalcanti 2000), but for most endemic species, detailed ecological studies are still urgently required. Table 1.1 reveals two species that stand out as being in particular need of studies of their ecology and conservation requirements: Blue-eyed Ground-dove *Columbina cyanopsis* and White-winged Nightjar *Caprimulgus candicans*.

STUDY SPECIES

The White-winged Nightjar *Caprimulgus candicans* is a small (19-21 cm, *c.* 47-56 g), sexually dichromatic caprimulgid of the campo grasslands of central South America. First mentioned by Azara (1805) as his “Ibiyau del alas y cola blancas” from Paraguay, but without date or locality, the male was first collected in 1823 from Oriçanga, São Paulo state, Brazil, and described as *Stenopsis candicans* (Pelzeln *in* Sclater 1866). An immature specimen collected in the 1820s from Cuiabá, Mato Grosso state, Brazil, was described as *Stenopsis langsdorfi* by Pelzeln (*in* Sclater 1866), although he himself noted that it was very possibly “only the young female of *Stenopsis candicans*”. No further specimens or records were obtained from Brazil until a series of sightings in the 1980s at Parque Nacional das Emas, Goiás state (Redford 1985, Collar *et al.* 1992, Sick 1993). An adult male collected in September 1987 at Estación Biológica del Beni, Yucuma province, Bolivia, represented the first record for that country (Davis & Flores 1994; Figure 1.1).



Figure 1.1 Map of central South America showing localities known for the White-winged Nightjar. White circles represent historical localities: 1 = Oriçanga; 2 = Cuiabá. Black circles represent modern localities: 3 = Parque Nacional das Emas; 4 = Estación Biológica del Beni; 5 = Reserva Natural del Bosque Mbaracayú; 6 = Laguna Blanca. Areas shaded dark and mid grey represent the Cerrado and Beni savannas respectively (source: www.worldwildlife.org/ecoregions).

On the basis of its small and potentially declining population, the White-winged Nightjar was classified as ‘Critical’ by Collar *et al.* (1994). Searches for the species at Beni, since the collection of the original male in 1987, have failed to produce further records (J. Hornbuckle *in litt.* 1998), but there have been consistent sightings at Emas (Rodrigues *et al.* 1999, A. Hass *in litt.* 2002). In September 1995, a population was discovered at the Reserva Natural del Bosque Mbaracayú (RNBM; see ‘Study site’), Canindeyú department, Paraguay (Lowen *et al.* 1996a, 1997), and later estimated to number between 40 and 130 individuals (Capper *et al.* 2000). The discovery of this population, and a re-evaluation of the numbers in Brazil, led to the species being downlisted to ‘Endangered’ in BirdLife International (2000), a decision later borne out by the discovery of a second Paraguayan population at Laguna Blanca, San Pedro department, in 2001 (Anon. 2002).

Prior to the discovery of the species in Paraguay, the ecology and conservation requirements of the White-winged Nightjar were extremely poorly known, with its threatened status based mainly on its small estimated population and the continuing destruction of its Cerrado habitats (Collar *et al.* 1992). Anecdotal observations from Emas suggested that it preferred areas of open grassland, and possibly even made local movements in response to fires (Collar *et al.* 1992), and this predilection for recently burnt areas was also noted in Paraguay by Lowen *et al.* (1997). Seven individuals, in

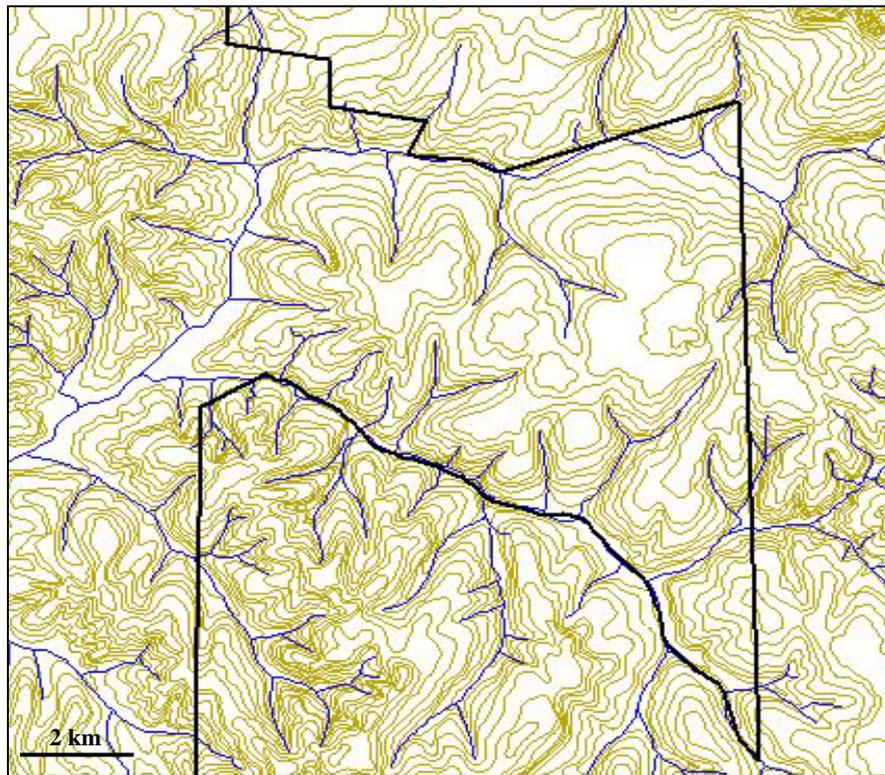
two distinct plumages, were captured at the RNBM during fieldwork in September and December 1995 (López Lanús *et al.* 1998), and observations were made of the display flights and territorial behaviour of breeding males (Clay *et al.* 2000). Between July and December 1997, further aspects of the species' breeding biology and general ecology were studied at the RNBM, as part of a conservation project designed to help develop a management plan for the site. The eggs, nest and plumage of the adult female were described for the first time, and some data were collected on the species' roosting and foraging behaviour (Clay *et al.* 1998, Capper *et al.* 2000). An injured male, captured in July 1997, was subsequently collected and the specimen (only the fourth known for the species) deposited in the Museo Nacional del Paraguay, Asunción.

In addition to its conservation importance, the White-winged Nightjar is also a fascinating and unusual member of its family, the Caprimulgidae (or true nightjars), a cosmopolitan group of insectivorous non-passerines with *c.* 90 species worldwide. As a primarily nocturnal family, nightjars are probably best known for their far-carrying calls and songs, which often provide the most reliable cues for their identification and location (Sick 1993, Holyoak 2001). When not vocalising, however, nightjars are extremely cryptic, with their camouflaged plumages helping them to avoid detection by predators at their daytime roosts. Nevertheless, many species show prominent white markings in the wings, tail or throat, which they display for the purposes of intra- and inter-specific communication, but which are concealed at rest (Mengel 1972, Bruce 1973, Cramp 1985). Most species show some sexual dimorphism in these markings, but the extreme dimorphism shown by the White-winged Nightjar led early naturalists to speculate that the type specimen was an albino variety (Pelzeln *in* Sclater 1866). Interestingly, the striking plumage of the study species is also accompanied by much-reduced vocalisations: the dull sounds produced during male display flights are apparently mechanical in origin (Clay *et al.* 2000).

STUDY SITE

In 1998-2001, I studied a population of White-winged Nightjars at the RNBM, Paraguay's most important site for the conservation of threatened bird species (Wege & Long 1995, Lowen *et al.* 1996b, Capper *et al.* 2000). Protecting a range of threatened habitats within its 64,405 ha, the greater part (*c.* 85%) of the reserve is forested, but it also encompasses *c.* 5,500 ha of open country habitats at Aguará Ñu (centred on 24°10'S, 55°17'W) on its easternmost edge. Aguará Ñu is a low plateau, 170-270 m above sea level, bounded on three sides by two rivers: the Arroyo Guyrá Kehá and the Río Jejui'mí (Figure 1.2). It constitutes a natural island of cerrado vegetation, flanked by forest to the south and west, and isolated from Paraguay's main areas of cerrado in the departments of Concepción and Amambay to the north-west (Jiménez & Knapp 1998). Its weathered, ultisol soils support a variety of habitats, including xerophytic woodland, Yata'i (*Butia paraguayensis*)

(a)



(b)

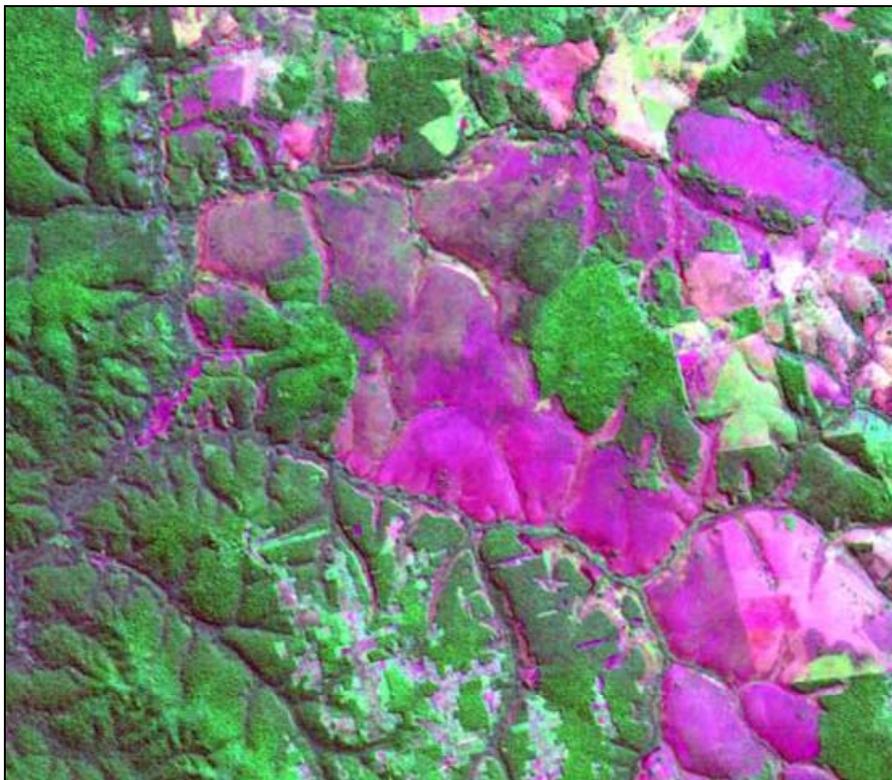


Figure 1.2 (a) Digital map of Aguará Ñu showing the boundary of the RNBM (thick black line), principal water courses and local relief; (b) Landsat satellite image of Aguará Ñu illustrating its status as a habitat island, bounded by the Arroyo Guyrá Kehá to the south, and the Río Jejui'mí to the north and west.

palm savanna, ‘campo cerrado’ (open grasslands with scattered shrubs, trees and palms), islands of forest, seasonally saturated grasslands, marshes and gallery forests.

The majority of fieldwork conducted during the current study focussed on an area of *c.* 400 ha in the southern sector of Aguará Ñu, where a series of shallow valleys drain southwards into the Arroyo Guyrá Kehá. The seasonally wet grasslands of the valley bottoms and lower slopes are dominated by grass (e.g. *Paspalum* spp.) and sedge (e.g. *Rhynchospora* spp.) species, and woody vegetation is almost entirely absent. The drier soils of the upper slopes and ridge tops support campo cerrado vegetation, consisting primarily of grasses and herbs, but with a scattering of shrubs (e.g. *Cochlospermum regium*, *Caryocar brasilense*), Yata’i palms, saplings and the occasional fully-grown tree (e.g. *Tabebuia ochracea* and *Annona* spp.). Palm density is lowest at the tips of the ridges in the south, where the campo cerrado is relatively open, but increases to the north as the campo cerrado grades into the dense palm cerrado of Aguará Ñu’s central ‘spine’. Termite mounds, 15-90 cm in height, are scattered liberally throughout the campo cerrado and wet grassland, and low anthills occur occasionally in the campo cerrado.

Wildfires are a regular occurrence at Aguará Ñu, particularly during the austral spring (i.e. August and September). The great majority are anthropogenic in origin – set by neighbouring landowners to clear cattle pasture and promote regrowth at the end of the dry season – but subsequently spread uncontrolled into the protected area. The extent to which these fires affect Aguará Ñu varies according to the climatic conditions and amount of combustible vegetation available. Recently, uncontrolled wildfires have burnt a significant proportion of Aguará Ñu’s grassland habitats in each of 1994, 1995, 1997 and 1999. In years with no spring burn, the grass species *Loudetia flammida* sprouts up to *c.* 2 m in height during the summer, dramatically altering the structure of many areas of campo cerrado (pers. obs.). Its flowering stems eventually die and dry out, but remain standing well into the following year, providing a highly flammable fuel source for the next fire. In 1999, the lack of burns the preceding year, and several nights with heavy frost (which killed much frost-intolerant vegetation), resulted in a large build-up of dry biomass, and a particularly extensive and fast-moving wildfire.

Located *c.* 75 km south of the Tropic of Capricorn, Aguará Ñu receives a continental, sub-tropical climate, with a hot wet season between October and February, and a cold dry season between June and August (Figure 1.3). The mean annual rainfall is 1,600-1,700 mm, occurring in a sporadic manner, with daily totals of up to 90 mm during the summer months (unpubl. data). The mean annual temperature is 21° C, with maximum daytime temperatures regularly reaching 40° C during the summer months, and frosts occurring on four or five nights every winter (Madroño Nieto & Esquivel 1997; pers. obs.).

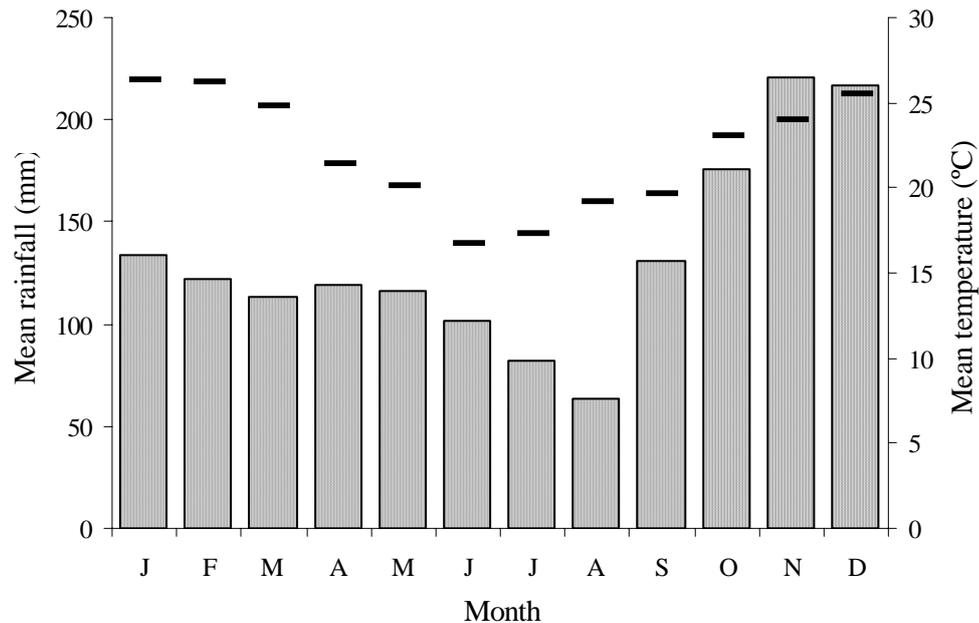


Figure 1.3 Mean monthly rainfall (histograms) and temperature (bars) for approximate area of the study site. Rainfall data for San Estanislao, San Pedro (24°39S, 56°24W); temperature data for Saltos del Guairá, Canindeyú (24°03S, 54°18W; source: www.worldclimate.com).

STRUCTURE OF THE THESIS

This thesis comprises four largely self-contained data chapters – each with its own summary, introduction, methods, results, discussion and conclusions – which can be read independently of each other. Nevertheless, each data chapter does assume some familiarity with the introductory information provided in the current chapter, and inevitably there is a certain amount of overlap between chapters, particularly in methodological matters.

Chapter 2 begins by providing the first detailed account of the morphometrics, plumages and moult of the White-winged Nightjar. Sexual differences in morphological measures are investigated, and the plumages of immature and adult birds of both sexes are described. The timing and duration of flight feather moult is analysed, and sex and age differences in moult strategies are highlighted. The white in the wing of adult male nightjars is quantified for the first time, and the suggestion that there is considerable inter-individual in its extent (López Lanús *et al.* 1998, Capper *et al.* 2000) is investigated.

Chapter 3 represents the first comprehensive overview of the breeding biology of the study species, based on data collected over the course of three breeding seasons. The spatial distribution of male territories is analysed in a quantitative manner, and related to topographical and social factors. Details are provided of the nuptial flight display performed by males at their display arenas, and inter- and intra-male variation in display rate is investigated. The species' nesting biology is

described using data from multiple nesting attempts, and the division of parental care between the sexes is documented. These data are used to critically assess the suggestion that the study population exhibits a 'landmark' or lek-mating system (Clay *et al.* 2000).

Chapter 4 investigates the spatial distribution of nightjars in greater detail. Radio-telemetry methods are used to document the ranging behaviour of breeding and non-breeding individuals, and a variety of analytical techniques is used to provide estimates of the size and configuration of home ranges. Habitat usage is inspected at two spatial scales – that of the overall home range, and when selecting foraging and roosting sites within ranges – and functional explanations are provided for deviations from random usage. Furthermore, to investigate the postulated preference of the study species for recently burnt areas (Collar *et al.* 1992, Lowen *et al.* 1997), an experimental burn (partially overlapping home ranges) is conducted, and the response of nightjars monitored.

In Chapter 5, the focus of the thesis shifts away from fieldwork, as the extreme dichromatic plumage of the study species is set in the context of the family Caprimulgidae as a whole. Using museum specimens, the extent of white markings in the wings, tail and throat of *c.* 70 caprimulgid species is assessed in a quantitative manner, and a measure of sexual plumage dimorphism is obtained for each species. Inter-specific variation in whiteness is related to species' ecological attributes, such as the structural density of their breeding habitats, to investigate the extent to which these may have influenced the evolution of plumage markings (e.g. Marchetti 1993). Sexual size dimorphism is also assessed, using data for wing and tail lengths from the literature. Patterns of plumage and size dimorphism are then analysed in the context of the information available on phylogenetic relationships and mating systems within the family.

Finally, in Chapter 6, the main findings and conclusions of the thesis are reviewed, and the ways in which the study species appears to be such an unusual member of its family are reiterated. The practical implications of the study for the conservation of the White-winged Nightjar and the management of its habitats are emphasised, and profitable avenues for further work and future conservation action are recommended.

STATISTICAL ANALYSIS

All statistical analyses in this thesis were undertaken using the software packages MINITAB 13 and SPSS 10. Prior to analysis, continuous data were tested for heterogeneity of variance using the Levene test, and for normality using the Kolmogorov-Smirnov test (Dytham 1999). If variables were not normally distributed, attempts were made to normalise them using square root or logarithmic (skewed data), or arcsine square root (percentages or proportions), transformations (Sokal & Rohlf 1995). Where this failed, non-parametric methods were used, following Siegel &

Castellan (1988), taking care to check the validity of statements of significance when sample sizes were small (Mundry & Fischer 1998). Where appropriate, data were analysed using multivariate tests, such as multiple linear and binary logistic regression. Means are quoted \pm one standard error throughout. Unless otherwise specified, statistical tests are two-tailed and significance was established at $P < 0.05$. If appropriate, non-significant trends are highlighted if $0.05 < P < 0.1$. Since the repeated use of a statistical test increases the probability of committing a Type I error, the sequential Bonferroni technique was employed to adjust the initial α level when making many simultaneous comparisons (Rice 1989). Categorical data were analysed using the G -test for goodness of fit when comparing data with an expected distribution, and the G -test of independence when comparing two or more sets of categorical data. Although the G -test is now considered to be superior on theoretical grounds to traditional chi-square methods (Dytham 1999), it was not supported by either of the statistical packages used, and so G statistics were calculated manually, following the methods detailed in Sokal & Rohlf (1995).

CHAPTER 2

PLUMAGES, MOULT AND MORPHOMETRICS OF THE WHITE-WINGED NIGHTJAR

SUMMARY

This chapter represents the first comprehensive summary of the plumage sequences, moult strategies and morphometrics of the White-winged Nightjar. Between 1998 and 2001, 49 nightjars (34 adults and 15 young birds) were captured and ringed in eastern Paraguay. The pre-definitive plumage of 'immature' nightjars was found to show many similarities with that of definitive females, although the two plumages were distinguishable using flight-feather shape and subtle differences in markings. Female nightjars bred when approximately a year old, while still in pre-definitive plumage, and only moulted into definitive plumage at the end of the breeding season. Male nightjars began moult into definitive plumage in September, at the very start of their first potential breeding season, and spent the majority of the season in a conspicuously intermediate state of moult. Males hence exhibited a form of delayed plumage maturation, a phenomenon known in relatively few other caprimulgids. Adult nightjars of both sexes replaced their flight feathers during a single post-nuptial moult between December and February. Primary moult lasted *c.* 65 days, but males began moult two weeks earlier than females. The primaries were moulted descendantly, from the innermost feather outwards. Secondary moult was serially ascendant, with two active moult centres, at S1 and S5 or S6, progressing inwards. Tail moult was rather variable, but apparently followed the sequence R1-R2-R5-(R3 or R4). Standard morphometric measures were obtained from seven adult female and 23 adult male nightjars. There was no evidence of significant sexual dimorphism in any of the four standard linear measures investigated (wing, tail, tarsus and bill), but female nightjars were 6% heavier than males. Sexual differences were also found in a novel measure of wing curvature: the outer primary of males was 19% more curved than in females. Definitive male nightjars showed considerable variation in whiteness, with co-efficients of variation for three measures of wing plumage 14 times higher than for four morphometric measures. An analysis of inter- and intra-male variation in plumage whiteness showed the effect of individual to be highly significant, although there was also a non-significant trend for age-related increases in white between consecutive definitive plumages.

INTRODUCTION

The plumage of birds serves a variety of purposes, most notably in flight, streamlining, insulation, waterproofing, camouflage and communication. Despite the strength and durability of feathers, plumage is inevitably subject to abrasion and eventually needs replacing through moult (Ginn & Melville 1983). Moult is an energetically expensive process because, in addition to the production of new feathers, it involves thermoregulatory and aerodynamic costs (Lindström *et al.* 1993, Swaddle & Witter 1997). As a consequence, most bird species show little, if any, overlap between moult and breeding, commencing moult shortly after the end of the breeding season (Foster 1975, Ginn & Melville 1983, Stutchbury & Morton 2001). However, more complicated moult strategies are shown by some long-distance migrants (Stresemann & Stresemann 1966) and species with distinct seasonal or status-related plumages (e.g. Rohwer 1977, Andersson 1983, Thompson 1991, McDonald 1993).

The White-winged Nightjar *Caprimulgus candicans* is a rare, sexually dichromatic species of the open country habitats of central South America. Only four specimens are known to exist in museum collections (Chapter 1), and until recently the species remained extremely poorly known in life. Adult male White-winged Nightjars show more white in the plumage than any other species in the family (Chapter 5), with most of the proximal part of the wing, and the four outermost pairs of tail feathers, predominantly white (Plate 2.1). This conspicuous plumage plays an important visual role in the nuptial flight displays of males (Clay *et al.* 2000; see also Plate 3.1), and observations suggest that there is notable inter-individual variation in its extent (López Lanús *et al.* 1998, Capper *et al.* 2000).

Although Holyoak (2001) treats the Cuiabá specimen (see Chapter 1) as an adult female, the original description (Pelzeln *in* Sclater 1866) and the shape of its tail feathers and outer primaries clearly identify it as an immature bird (N. Cleere *in litt.* 2002). A formal description of the adult female plumage has yet to be published, but, broadly, females are browner than males and lack the white plumage of the wings and tail (Capper *et al.* 2000; Plate 2.1). A further plumage, postulated to be that of an immature male, was described following the capture of an individual at the site of the current study in December 1995 (López Lanús *et al.* 1998). The only information published on moult in the species is that the type specimen was nearing the end of a complete moult when collected (early January), and that the pattern of feather replacement suggests that the primaries are moulted descendantly and the rectrices centrifugally (Cleere 1998).

In this chapter, I present the first comprehensive overview of the plumages, moult strategies and morphometrics of the White-winged Nightjar, based on data collected during a three-year study in eastern Paraguay. Differences between the plumage of young and adult birds are outlined, and

primary moult data are inspected for evidence of different moult strategies between age and sex classes. The combined data are interpreted to derive a summary of the species' moult and plumage sequences. Less formal data are also presented on moult patterns in the secondaries and rectrices. Standard morphometric measures and an estimate of wing curvature are presented for adults of both sexes, and inspected for sexual size dimorphism. Finally, attempts are made to quantify the 'whiteness' of the wing plumage of adult males, and inter- and intra-male variation in this measure are investigated, with particular emphasis on their relationship with age.

METHODS

Fieldwork was conducted over the course of three field seasons between 1998 and 2001 at Aguará Ñu in eastern Paraguay (Chapter 1). White-winged Nightjars (hereafter 'nightjars') were located at night by their reflective eye-shine in the beam of a powerful torch, visible from distances of *c.* 150 m under certain conditions. Once located, nightjars were captured with a small hand-held net, whilst dazzled by the light of the torch (see also Jackson 1984). All adult birds were fitted with an individually numbered metal tarsus ring and a coloured plastic ring. Since it was not always possible to see the latter clearly, a small, uniquely shaped piece of reflective tape was affixed to one of the non-central tail feathers. This mark was unobtrusive when birds were at rest during the day, but immediately conspicuous when illuminated with a torch at night.

Plumages and moult

The terminology used herein for plumages and moult broadly follows Cramp & Simmons (1977), incorporating the amendments proposed by Ginn & Melville (1983). However, when referring to plumages, the terms 'definitive' and 'pre-definitive' are used in preference to 'adult' and 'immature', to avoid potentially unwarranted implications regarding the reproductive maturity of birds (Humphrey & Parkes 1959). Adult caprimulgids typically exhibit broad, rounded or square-tipped feathers, whereas the retained juvenile feathers of young birds are narrower, more pointed and often pale-tipped (Rohwer 1971, Baker 1993, Holyoak 2001). These characters were also found to serve as useful indicators of age in the study species (see Results), and hence it was possible to distinguish nightjars in pre-definitive and definitive plumage on the basis of feather shape alone. Most nightjar species undergo a 'post-juvenile moult' of the contour feathers (but not flight feathers) a few weeks after fledging (Holyoak 2001). No data were collected during the current study on the contour moult of young nightjars, and hence no distinction is made between juvenile and pre-definitive birds: the term 'pre-definitive' is used herein for any fledged bird retaining juvenile flight feathers. Although it was impossible to determine the sex of pre-definitive birds, the presence or absence of white in the wings and tail easily sexed nightjars in definitive plumage.

In the current study, primary feathers were numbered descendantly (innermost primary is 'P1'), secondaries were numbered ascendantly (outermost secondary is 'S1'), and rectrices were numbered from the centre of the tail outwards (Ginn & Melville 1983). Like other caprimulgid species (Baker 1993), White-winged Nightjars have 10 primaries and 13 secondaries on each wing, and 10 rectrices. Where feasible, all captured nightjars were inspected for evidence of flight feather moult, scoring the primaries from 0 (old) to 5 (new), according to their stage of growth (Ginn & Melville 1983). When time permitted, less formal data were also collected on secondary moult. The total scores for each wing were averaged to give a mean primary 'moult score' between 0 and 50. The rectrices were inspected and scored in a similar manner. Before undertaking analyses, primary and rectrix scores were divided by 50 and 25 respectively, to give 'moult indices' between 0 (not yet started moult) and 1 (completed moult).

The following parameters of primary moult were estimated using an adaptation of the model proposed by Underhill & Zucchini (1988): mean start date (μ) and standard deviation (σ) of moult, and mean duration (τ) of moult in days. The model assumes a linear relationship between moult index and time, whereas, in practice, raw moult scores typically show a sigmoidal increase (Underhill & Zucchini 1988, Rothery *et al.* 2001). A more linear increase with time may be obtained by using a moult index that reflects percentage feather mass grown (e.g. Summers *et al.* 1983, Underhill *et al.* 1992, Rothery *et al.* 2001). Unfortunately, data on the relative masses of White-winged Nightjar primaries were not available for such an adjustment in the current study, and a linear increase in raw moult index with time was assumed. The moult data collected were distributed between seasons and 'stages' of moult in a highly uneven manner (see Results), and so it was impractical to investigate annual variation in moult parameters. However, a model selection procedure was used that assessed variation in moult parameters among the three 'age/sex classes' for which sufficient samples were available: adult females, adult males and first-year males. Too few data were collected from first-year females to merit their inclusion in the analysis.

Morphometric measures

The following standard morphometric measures were taken from captured nightjars, following Baker (1993): mass; wing length (minimum wing chord); tail length (from base of under tail coverts); bill (tip to anterior edge of nostril); and tarsus. Mass was measured to 0.5 g using a 100 g Pesola balance. Wing and tail length were measured to 0.5 mm with a stopped and square-ended rule respectively. Bill and tarsus were measured to 0.1 mm using dial callipers. The measurement for 'tarsus' was taken from the rear of the tibia, since the notch at the back of the intertarsal joint is difficult to locate in caprimulgid species.

The wing of definitive male White-winged Nightjars is noticeably modified in shape compared to most Neotropical nightjars, and it has been postulated that the curved, rigid outer primaries produce the mechanical noise that accompanies male display flights (Clay *et al.* 2000, Cleere 2002). To estimate the extent of primary curvature, a novel measurement was developed for the current study. A square-ended rule was held against the outermost primary, at the level of the greater primary covert, with its edge tangential to the feather's outer web. The distance from the tip of the primary to the extension of the rule was then measured, using dial callipers, to estimate the deflection of the feather tip from the tangent (Figure 2.1). The length of the straightened primary was also measured, and an angle was derived approximating the curvature of the feather.

To avoid pseudoreplication, analyses involved only the first measurement of each morphometric character from any individual. The exception to this was mass, for which a mean value across adult captures was calculated for each individual, as intra-individual variation could be expected between captures. Data from gravid females adjudged to have been within 72 hours of laying were excluded from the analysis.

Male plumage whiteness

Previous assessments of male plumage whiteness in the White-winged Nightjar have been based solely on qualitative observations or the inspection of photographs (López Lanús *et al.* 1998, Capper *et al.* 2000). In the current study, attempts were made to measure male whiteness in a quantitative manner, and hence provide a more rigorous assessment of inter- and intra-male variation. Only a small number of studies have investigated variation in white markings in nightjar species (Ingels & Ribot 1982, Forero *et al.* 1995, Forero & Tella 1997, Aragonés *et al.* 1999), and in each case the white occurred as discrete patches. In contrast, the white plumage in the wing and tail of the White-winged Nightjar is extensive and poorly defined, and hence more difficult to quantify.

Photographs of captured males suggested that it might be possible to obtain a surrogate for wing whiteness by measuring the extent of black markings within and adjoining the white plumage of the wing. Two main areas were identified in which there was notable variation: the point at which the arc of white bisects the trailing edge of the wing; and the extent of black markings on the edges and tips of the primaries and primary coverts. Three measures were chosen to quantify this variation: (a) 'P2DEP' – the depth of black at the tip of primary two; (b) 'P3DEP' – the depth of black at the tip of primary three; (c) 'C10DEP' – the depth of black at the tip of the tenth primary covert (Figure 2.1). All three characters were measured along the rachis to the nearest 0.1 mm using dial callipers. Characters were re-measured each time an individual was recaptured in a fresh plumage (i.e. following a complete moult).

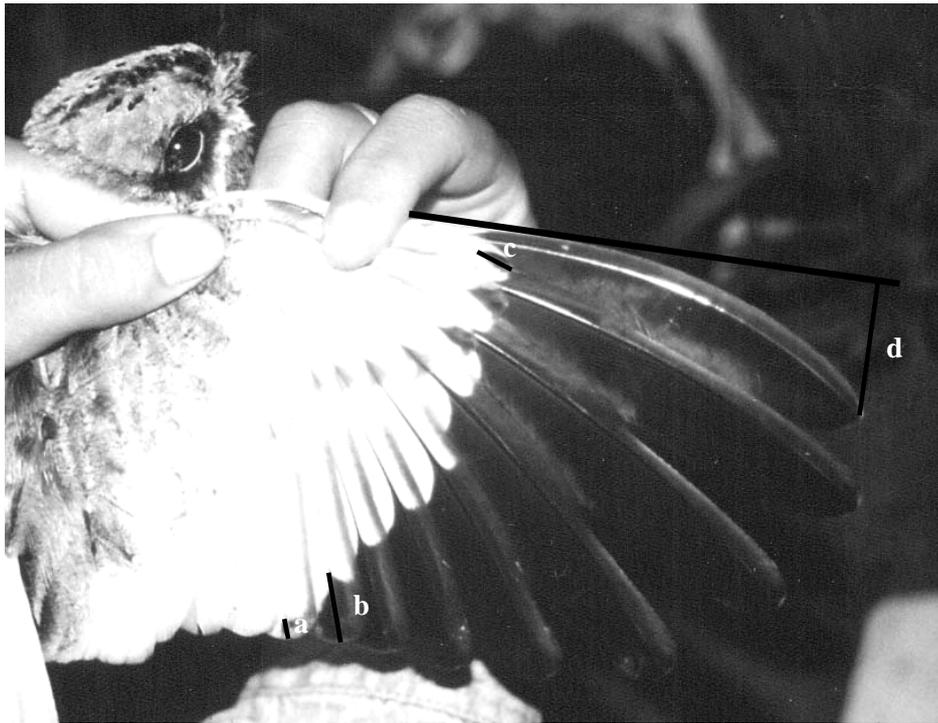


Figure 2.1 Wing of definitive male nightjar, illustrating measures of plumage and primary wing curvature taken during the current study: (a) ‘P2DEP’; (b) ‘P3DEP’; (c) ‘C10DEP’; (d) deflection of P10 tip from the tangent.

Statistical analysis

All continuous data were tested for normality and homoscedasticity prior to analysis with standard parametric and non-parametric univariate tests (Chapter 1). Statistical significance was set at $P < 0.05$ unless otherwise specified. Means are given \pm one standard error, except for measures of male plumage whiteness, where the standard deviation and coefficient of variation are provided. As measures of whiteness were found to be significantly inter-correlated, a principal component analysis (PCA) was used to obtain uncorrelated principal components (PCs), summarising the dimensions of greatest variation in the data (Manly 1986). The sum of the eigenvalues (standardised variances of the components) in a PCA equals the number of components, hence only PCs with an eigenvalue > 1.0 were considered significant, since only they explain more variation than the original variables. When interpreting the extracted PCs, only variables with loadings $\geq |0.50|$ were considered practically significant (Hair *et al.* 1995).

Primary moult data were analysed in Systat 5.03 (Wilkinson 1990), using a maximum-likelihood fitting of an adaptation of the moult model of Underhill & Zucchini (1988). Models were fitted with all, none, and every combination of the three parameters able to vary among the three age/sex classes. The minimum adequate model (MAM) – i.e. the model providing an adequate fit to the data without incorporating an unwarranted number of terms – was selected using a stepwise

procedure, with entry and removal probabilities set at $P < 0.05$. At each step, the term whose inclusion resulted in the greatest change in deviance was entered into the model, providing that its inclusion significantly improved the fit of the model. Significance was tested using likelihood ratio tests in which the difference in deviance ($-2 * \log_e$ likelihood) between models with and without terms was treated as χ^2 , with degrees of freedom equal to the number of parameters being added (Crawley 1993). The MAM was achieved when no further terms met the criteria for entry or removal.

RESULTS

In total, 49 nightjars were captured and ringed between 1998 and 2001: 34 adults and 15 individuals caught only as young birds (either as nestlings or fledged young). A wing and the tail of a definitive female found dead in January 1999 were salvaged and donated to the Museo Nacional de Historia Natural del Paraguay in Asunción.

Plumages

Five fledged nightjars in pre-definitive plumage were captured during the study. One young bird, captured on 30 October 1998, had not completed flight-feather growth: its primaries and rectrices were all approximately the same length, but still in pin at the base, indicating simultaneous feather replacement. The other four individuals had completed flight-feather growth, but clearly showed the pointed- and pale-tipped outer primaries and rectrices characteristic of juveniles. Photographs of captured nightjars confirmed that, aside from feather shape, the plumages of definitive females and pre-definitive birds (of either sex) were superficially very similar. Although no clear-cut differences were identified, definitive females did apparently show deeper unmarked, and somewhat grey-tinged, tips to their outermost primaries; in pre-definitive birds, the tawny barring extended further down towards the feather tip. Supporting evidence was obtained from a female captured in successive years and photographed in pre-definitive and definitive plumages (Plate 2.1). A further potential difference was a more intricate pattern and grey wash on the rectrices of definitive females. Furthermore, some young birds – possibly immatures (*sensu stricto*) in fresh plumage following the post-juvenile moult – showed conspicuously pale downy tips to the breast feathers, median and lesser coverts, giving them a ‘flecked’ appearance (Plate 2.2).

One female (F066), first captured in pre-definitive plumage in August 1999, made two successful breeding attempts during September-December 1999 (Chapter 3), and only began moult into definitive plumage at the end of its first breeding season. Young males, meanwhile, showed a notably different moult and plumage sequence. A male captured in pre-definitive plumage in December 1998 was recaptured in September 1999, when it was found to be moulting into the white definitive plumage. Three other males were also captured during the breeding season in this

conspicuously intermediate (but active) state of moult, with a mixture of retained brown and new white wing feathers (Plate 2.2). A male ringed as a chick in October 2000, and recaptured in December 2001 when it had almost completed moult into definitive male plumage (J. Mazar Barnett *in litt.* 2002), confirmed suspicions that males moulted into the definitive plumage approximately one year after hatching.

Flight-feather moult

Primary moult data were collected during 88 captures of 36 nightjars between October 1998 and July 2001. Data on secondary and rectrix moult were also collected for a subset of these birds. A first-year male, captured on 26 September 1999, was the earliest bird to show flight-feather moult; the earliest capture of an adult in active moult was on 11 November (a male in 1998). The latest date on which an individual was captured in primary moult was 24 February 2001 (an adult male). The majority of nightjars were either yet to commence primary moult (48%) or already in active moult (43%) at the time of capture, with only a small proportion of captures (9%) having already completed moult (Table 2.1).

Table 2.1 Number of nightjar captures scored for primary moult, by ‘stage’ of moult and season.

Season	Number of captured nightjars			Total
	yet to moult	in active moult	completed moult	
Oct 98 - Jan 99	10	25	3	38
Aug 99 - Dec 99	20	6	0	26
Aug 00 - Apr 01	12	7	5	24
Overall	42	38	8	88

The MAM was found to be that in which the start date ($\chi^2_{(2)} = 61.66$, $P < 0.001$) and mean duration ($\chi^2_{(2)} = 7.78$, $P < 0.05$) of moult varied significantly among age/sex classes, but the standard deviation did not ($\chi^2_{(2)} = 4.74$, $P > 0.05$). Although it was not feasible to investigate inter-season variation in moult parameters, inspection of plots of moult scores did not reveal any obvious annual variation after accounting for age/sex differences. Adult male nightjars began primary moult two weeks earlier than adult females, although estimates of moult duration for the two sexes were broadly similar (mean: 65.5 ± 2.6 days; Table 2.2). First-year males commenced moult *c.* 75 days earlier than adult males, and took 59% longer than adult birds to complete moult (Figure 2.2).

Table 2.2 Estimates (standard errors) in days of parameters of primary moult for three age/sex classes of nightjar captured between 1998 and 2001.

Age/sex class	<i>n</i>	Mean start date (μ)	SD (σ)	Duration (τ)	Mean completion date ^a
First-year males	7	18 September (14.8)	11.2 (2.8)	99.7 (20.1)	27 December
Adult males	55	3 December (5.2)	11.2 (2.8)	62.9 (12.6)	4 February
Adult females	18	17 December (10.1)	11.2 (2.8)	68.1 (18.1)	23 February

^a No standard error provided since derived from start dates and durations, not calculated by model.

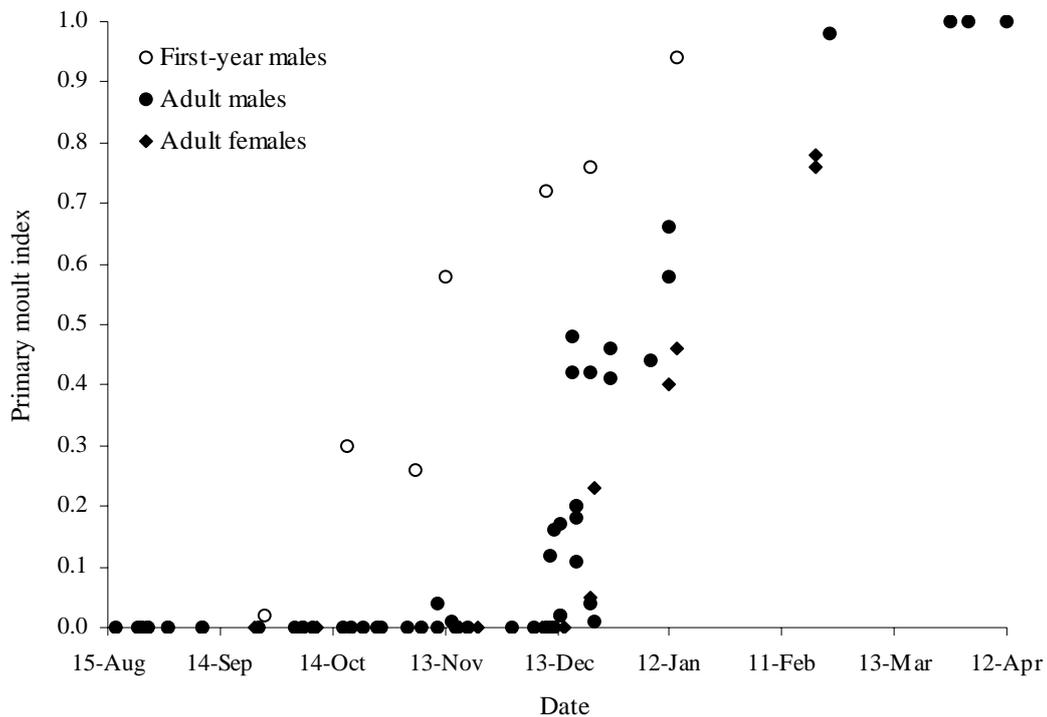


Figure 2.2 Primary moult index *versus* date for nightjars captured between 1998 and 2001, illustrating differing moult strategies of first-year males and adult males and females.

Primary moult progressed descendantly, from the innermost primary (P1) outwards. The only exceptions to this were two individuals that each dropped a single primary (on one wing) out of sequence. The limited data collected on secondary moult suggested that it was ‘serially ascendant’, with two active moult centres progressing inwards at S1 and S5 or S6.

Patterns of tail-feather moult were less easy to characterise, with asymmetry relatively common and a more variable sequence of feather replacement than for primary moult. However, the data suggested a potential rectrix moult sequence of R1-R2-R5-(R3 or R4). There was a significant positive correlation between rectrix and primary moult index for nightjars captured during active moult (Spearman’s rank correlation: $r_s = 0.742$, $n = 35$, $P < 0.001$), although rectrix moult typically commenced somewhat after the onset of primary moult.

Morphometric measures

Morphometric measures were obtained from seven adult female and 23 adult male nightjars. All six characters inspected showed some overlap between the sexes, with no significant sexual differences in any of the four standard linear measures (Table 2.3). Even though the weights of four gravid females (mean: 65.1 ± 1.7 g; range: 62.5–70.0 g) were excluded from the analysis, females

were *c.* 6% heavier than males. There were also significant differences in the estimate of wing curvature: male wings were *c.* 19% more curved than female wings.

Table 2.3 Morphometric measurements of adult male and female nightjars.

Measure	Male			Female			Significance ^a
	Mean ± se	Range	<i>n</i>	Mean ± se	Range	<i>n</i>	
Mass (g)	50.6 ± 0.4	47.0-54.5	23	53.5 ± 0.8	51.5-55.5	5	$t_{26} = 3.03, P = \underline{0.005}$
Wing (mm)	149.5 ± 0.7	143.0-156.0	22	148.0 ± 1.1	145.0-152.0	6	$t_{26} = -1.02, NS$
Bill (mm)	6.2 ± 0.1	5.2-6.7	22	6.4 ± 0.2	6.0-6.7	5	$t_{25} = 1.10, NS$
Tarsus (mm)	23.9 ± 0.2	21.9-25.2	22	24.2 ± 0.2	23.2-24.9	6	$t_{26} = 0.91, NS$
Tail (mm)	103.6 ± 0.7	98.0-110.0	22	99.7 ± 1.4	95.0-104.0	6	$t_{26} = -2.67, P = 0.013$
Wing curvature (°)	16.6 ± 0.3	14.0-18.5	20	14.0 ± 0.9	11.4-15.9	5	$t_{23} = -3.59, P = \underline{0.002}$

^a From unpaired *t*-tests. Values underlined indicate table-wide significance at an adjusted initial α level of 0.008 (Rice 1989).

Male plumage whiteness

The three measures of wing plumage chosen as surrogates for wing whiteness varied considerably amongst males: their coefficients of variation were 14 times larger on average than those for standard linear morphometric measures (47.6 ± 15.9 versus 3.4 ± 0.7 ; Mann-Whitney *U*-test: $U = 18$; $n_1 = 3$; $n_2 = 4$; $P = 0.029$; Table 2.4).

Table 2.4 Coefficients of variation for measures related to male plumage whiteness compared to standard morphometric measures.

Measure (mm)	Mean ± sd	Range	Coeff. var.	<i>n</i>
<i>Plumage</i>				
P2DEP	4.6 ± 3.5	0.0-13.4	76.9	22
P3DEP	14.2 ± 6.2	5.8-30.2	43.4	18
C10DEP	8.3 ± 1.9	4.7-11.0	22.4	22
<i>Morphometric</i>				
Wing	149.5 ± 3.3	143.0-156.0	2.2	22
Bill	6.2 ± 0.3	5.2-6.7	5.3	22
Tarsus	23.9 ± 0.8	21.9-25.2	3.2	22
Tail	103.6 ± 3.1	98.0-110.0	3.0	22

The three plumage measures were highly inter-correlated (Pearson correlation matrix: all $r > 0.5$, all $P < 0.05$), and so a PCA was used to obtain independent components. Only the first principal component (PC1) had an eigenvalue greater than 1.0, but it alone accounted for *c.* 76% of the total variance (Table 2.5). As PC1 showed high negative, and almost equal, loadings for all three plumage measures, it was interpreted as an ‘overall whiteness score’ for subsequent analyses.

Table 2.5 Results of a PCA carried out on three inter-correlated measures of male plumage.

Variables	PC1	PC2	PC3
P2DEP	<u>-0.597</u>	-0.110	-0.795
P3DEP	<u>-0.573</u>	-0.635	0.519
C10DEP	<u>-0.562</u>	0.765	0.315
Eigenvalue	2.29	0.43	0.28
Variance (%)	76.4	14.2	9.4
Cumulative variance (%)	76.4	90.6	100.0

Values underlined indicate loadings $\geq |0.50|$ used in the interpretation of PC1 (see Methods).

Although it was not possible to determine the absolute age of definitive male nightjars, eight individuals were captured in two or more seasons in ‘consecutive’ definitive plumages (i.e. separated by one complete post-nuptial moult). To investigate the relative importance of inter- and intra-male variation in plumage whiteness, a two-way ANOVA was conducted on overall whiteness scores, with individual and plumage/year as factors. The effect of individual was found to be highly significant ($F_{7,12} = 87.23$, $P < 0.001$), and there was also a strong trend for an effect of plumage/year ($F_{3,12} = 3.26$, $P = 0.06$), although in practice only certain males showed consistent increases in whiteness with consecutive plumages (e.g. ‘M008’ in Figure 2.3).

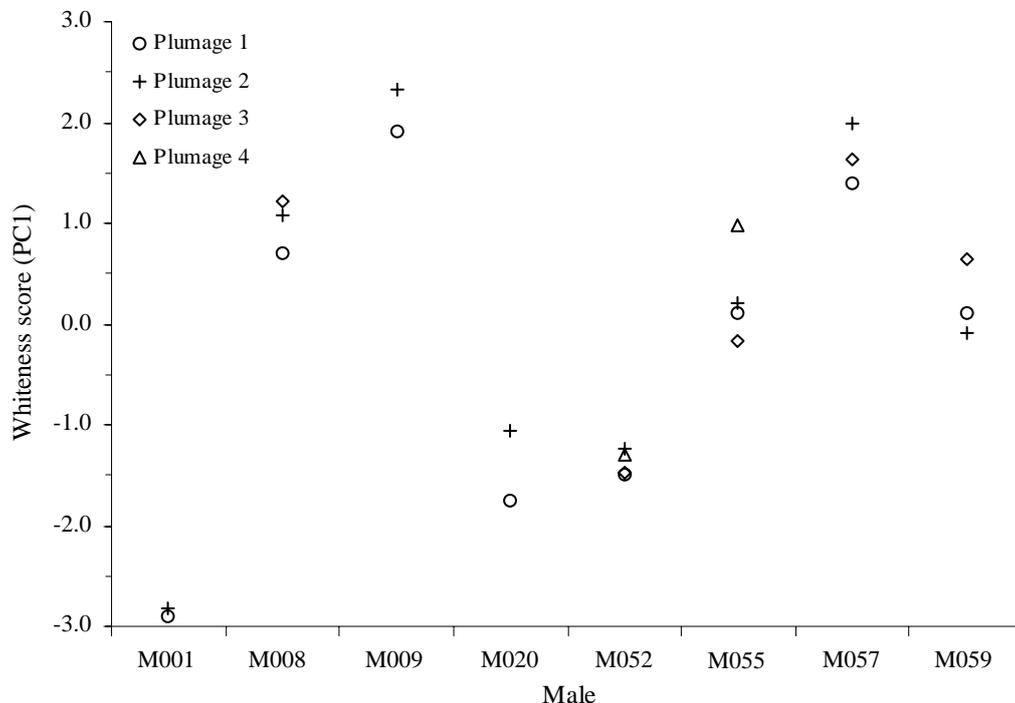


Figure 2.3 Inter- and intra-individual variation in whiteness score for eight male nightjars captured in two or more consecutive definitive plumages. ‘Plumage 1’ = score in first year measured; ‘Plumage 2’ = score in second year measured, etc. Higher scores for PC1 indicate whiter plumage.

DISCUSSION

Although the plumage of pre-definitive White-winged Nightjars differed little from that of definitive females, with experience the two could be distinguished using subtle differences in feather shape and markings. Nevertheless, no evidence was obtained to suggest that it was possible to determine the sex of pre-definitive birds on the basis of plumage alone. None of the pre-definitive nightjars captured during the current study showed the all-dark outer primary of the “immature male” captured and described in December 1995 (López Lanús *et al.* 1998), suggesting the latter may have been a bird in slightly aberrant plumage. A definitive male captured and photographed in November 1997 showed an aberrant all-white primary (P9) on the right wing (R. Clay *in litt.* 1998). The specimen collected from Cuiabá in the 1820s, and tentatively identified as a “young female” by Pelzeln (in Sclater 1866), has no supporting gonad data on the label (N. Cleere *in litt.* 2002), and so inferences regarding its sex should be treated with caution.

Definitively plumaged White-winged Nightjars replaced their flight feathers during a single post-nuptial moult, between December and February. No evidence was obtained during this or previous studies (Capper *et al.* 2000) for delayed or arrested moult, strategies more typical of migratory species (Stresemann & Stresemann 1966, Ginn & Melville 1983, Holyoak 2001). Primary moult was found to progress descendantly, as in various other nightjar species (e.g. Stresemann & Stresemann 1966, Rohwer 1971, Herremans & Stevens 1983, Cramp 1985, Gargallo 1994), and secondary moult was serially ascendant, one of three common secondary moult strategies in caprimulgids (Herremans & Stevens 1983). Small sample sizes precluded firm conclusions regarding tail moult, but rectrices were apparently replaced in the sequence R1-R2-R5-(R3 or R4), as also documented for Grey Nightjars *Caprimulgus indicus* (Holyoak 2001).

A schematic summary of the moult strategies and plumage sequence of male and female White-winged Nightjars during their first two-and-a-half years of life is presented in Figure 2.4. The timing and duration of moults of young males and definitive birds of both sexes were obtained during the current study (Table 2.2). Too few young females were captured to justify their inclusion in the analysis, but they were assumed to behave like definitive females for the purposes of this summary. No quantitative data were collected on the post-juvenile moult during the current study, but this moult is represented in Figure 2.4 on the basis of knowledge of the species’ breeding season (see Chapter 3). No evidence was obtained to suggest that pre-definitive nightjars underwent any flight-feather moult between the post-juvenile moult and the subsequent moult into definitive plumage. Photographs of a young male captured in December 1998, shortly after fledging, confirmed that it still retained the same outer primaries when it was recaptured in September 1999, mid-way through moult into definitive plumage.

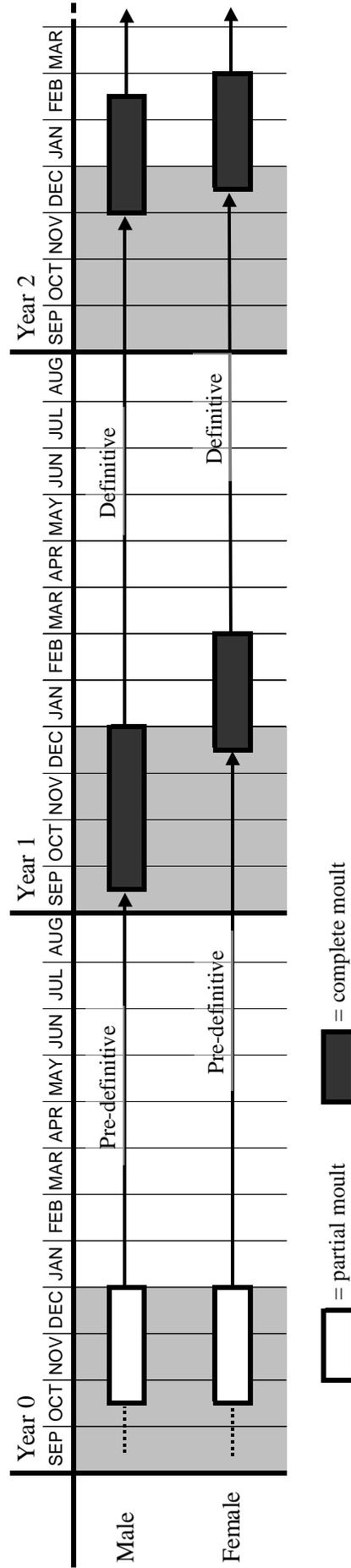


Figure 2.4 Schematic summary of the moult strategies and plumage sequence of male and female nightjars during the first two-and-a-half years following fledging (breeding season of 'Year 0'). Months shaded pale grey indicate the species' breeding season, but note that, in practice, males appear not to breed until 'Year 2' (Chapter 3).

Figure 2.4 highlights some important differences between the moult strategies of male and female White-winged Nightjars. Females were shown to breed when approximately one year old, while still in pre-definitive plumage, only moulting into definitive plumage at the end of the breeding season. Young males, meanwhile, began moult into the characteristic white definitive plumage in September, and spent the majority of the breeding season in a conspicuously intermediate state of moult; no evidence was obtained to suggest that they bred successfully (Chapter 3). Males hence exhibited a form of delayed plumage maturation, a development pattern whereby individuals of one sex (most commonly males) do not attain definitive breeding plumage until after their first potential breeding season (Hill 1996). This phenomenon is particularly well studied in temperate passerine species (e.g. Hill 1988, Rohwer & Butcher 1988, Thompson 1991), but is now recognised as being geographically and taxonomically more widespread (Chu 1994, Conover *et al.* 2000, Stutchbury & Morton 2001). Whilst not well documented in the Caprimulgidae, delayed plumage maturation is also shown by males of the two *Macrodipteryx* nightjar species, which show elaborate wing ornaments in definitive plumage (Stresemann & Stresemann 1966).

Once they attained definitive plumage, males and females showed broadly similar patterns of moult, undergoing a single complete moult at the end of each breeding season. Moult involves substantial energy expenditure (e.g. Lindström *et al.* 1993), and rarely shows any significant temporal overlap with other energetically costly activities such as breeding (Ginn & Melville 1983, Hemborg 1999). Although a few nesting attempts last into late December, the majority are completed by the middle of the month (see Chapter 3), around the date the average female began moult. Males, meanwhile, commenced moult two weeks earlier, and this difference in timing between the sexes almost certainly reflected their differing involvement in parental duties (Chapter 3; see also Jenni & Winkler 1994, Svensson & Nilsson 1997, Hemborg 1999).

The summary of morphometric measurements presented in the current study represents the most comprehensive provided to date for the White-winged Nightjar, and shows close agreement with previous studies (López Lanús *et al.* 1998, Capper *et al.* 2000; though note the different method of measuring ‘tarsus’ *cf.* López Lanús *et al.* 1998). Despite the extreme sexual dichromatism shown by the species, males and females were essentially monomorphic for all four standard linear measures investigated. Females were apparently significantly heavier than males, but the difference was slight (*c.* 6%), and may simply have resulted from the inclusion in the analysis of females carrying small, undetectable eggs or food boluses for chicks. Nightjars have very large stomachs, and when full, they may account for 20-25% of their body weight (Jackson 2000a). Significant sexual differences were, however, found for an estimate of wing curvature, with males showing *c.* 19% more curved outer primaries than females. This finding supports the suggestion of Clay *et al.* (2000) that the rigid, curved and slightly club-shaped outer primaries of males are involved in

the production of the mechanical noises that accompany male nuptial flight displays. A young male, moulting into definitive plumage but still retaining five or six juvenile outer primaries, was noted to produce a high-pitched and weak display noise (Chapter 3).

Although it proved necessary to measure the extent of black markings, rather than quantify the area of white, the results of the current study supported previous suggestions of notable variation in plumage whiteness among definitive males (López Lanús *et al.* 1998, Capper *et al.* 2000; Plate 2.2). Coefficients of variation for male plumage measures in the current study were over ten times higher than those for standard linear morphometric measures, which typically range between 2 and 6% (e.g. Alatalo *et al.* 1988, Evans & Barnard 1995). Similarly high coefficients of variation (11-52%) were found in a study of variability in the white wing and tail patches of Red-necked Nightjars *Caprimulgus ruficollis*, and taken to suggest that the patches were related to sexual selection (Forero & Tella 1997). Furthermore, a number of other studies have suggested that the size of nightjar wing and tail patches may be related to age (Ingels & Ribot 1982, Forero *et al.* 1995, Aragonés *et al.* 1999), and hence represent a signal of male quality and experience. Although it was not possible to determine the absolute age of males captured only as definitive birds in the current study, potential age-related changes in whiteness were investigated using measures from a subset of males captured in consecutive definitive plumages. Whilst this analysis did show a non-significant trend for the effect of age, there was no evidence for a consistent increase in whiteness with age when considering males individually. The notable variation within the population as a whole hence seems likely to be a result of inter-individual differences in whiteness rather than age-related changes.

CONCLUSIONS

This chapter has provided the first comprehensive overview of the morphometrics, moult strategies and plumage sequences of the White-winged Nightjar. Despite the species' conspicuous sexual dichromatism, the sexes were found to be essentially monomorphic for the standard morphometric measures inspected. Sexual differences were apparent, however, in a novel measure of wing curvature, and considerable inter-male variation was noted in measures of male plumage whiteness, suggesting that the latter may be sexually selected. Young male nightjars were shown to exhibit a form of delayed plumage maturation, whereby they spent the majority of their first potential breeding season in a conspicuously intermediate state of moult. Numerous hypotheses have been proposed to explain the adaptive significance of delayed plumage maturation (see Chapter 6), the central tenet of many being that males can expect very low reproductive success if they attempt to breed in their first year. The validity of this assumption depends, amongst other things, on the mating system of the species in question, and it is the breeding biology of the White-winged Nightjar that I investigate in Chapter 3.



(c)



(d)



(a)



(b)

Plate 2.1 Plumages of the White-winged Nightjar: (a) definitive male; (b) definitive female; (c) and (d) close-up of the wing of a female nightjar in pre-definitive and definitive plumages, showing subtle differences in feather shape and markings.



Plate 2.2 Plumages and moult: (a) young nightjar in fresh plumage following the post-juvenile moult; (b) first-year male in process of moulting from pre-definitive to definitive plumage; (c) and (d) wing of two definitive males, showing inter-individual variation in wing whiteness.

CHAPTER 3

BREEDING BIOLOGY OF WHITE-WINGED NIGHTJARS IN PARAGUAY

SUMMARY

This chapter presents the first detailed description of the breeding biology of the White-winged Nightjar *Caprimulgus candicans*, based on data collected over the course of three breeding seasons between 1998 and 2000. Male nightjars defended small display territories situated on the upper slopes of ridgelines in southern Aguará Ñu. Each territory contained one or more ‘arenas’ at which the male conducted his display activity. There was some evidence to suggest that display territories were established at traditional sites. The average nearest-neighbour distance between male display arenas was 254 ± 8 m. Aggregation indices confirmed that arenas were significantly clustered within the survey area in all three seasons. Within display territories, males apparently selected arenas on the basis of their structural characteristics: mounds used as arenas were significantly lower and broader than random mounds. Males were engaged in display activity from late August to early January. On average, males performed 0.54 ± 0.04 display flights per minute, but there was considerable intra-male variation in overall display rate. Following a burst of activity upon their dusk arrival at display arenas, male display rate was best explained by ambient levels of moonlight. Details are provided of a previously undescribed insect-like “tik tik” call produced by males when inactive on their display territories. Nine breeding attempts, by four females, were documented during the 1999 and 2000 seasons. Females made two nesting attempts per season, using a different site (360 ± 31 m apart) for each attempt. The clutch of two eggs was laid directly on the ground, adjoining a small access ‘clearing’, in either campo cerrado or wet grassland vegetation. The first egg was laid within two days of a full moon for all seven clutches for which laying date was confirmed. Incubation, brooding and chick provisioning duties were carried out exclusively by the female: on no occasion was a male observed at the nest site. Eggs hatched after a modal incubation period of 19 days. Some data are presented on the growth rate of chicks, with the evidence suggesting that ‘fledging’ occurred after *c.* 19 to 20 days. The amplified fragment length polymorphism (AFLP) technique was used to identify a single set of probable parents for eight chicks from five broods. For each brood, the postulated father had a display territory within 450 m of the nest site, though he was not necessarily the nearest territory-holding male. Overall, the evidence strongly suggested that the study population of White-winged Nightjars practises a polygynous mating system, and the possibility that it exhibits an exploded lek or ‘landmark’ mating system is discussed.

INTRODUCTION

Due in no small part to their cryptic plumage and largely nocturnal habits, the Caprimulgidae (true nightjars) are comparatively under-studied as a family. Their breeding biology in particular is poorly known, and for many species the only published data are either anecdotal in nature or based on single nesting attempts. Nevertheless, studies of the better-known species have shown them to be generally ground-nesting, with a clutch of one or two eggs, and an essentially monogamous breeding system (Cleere 1999, Holyoak 2001). The Caprimulgidae are also one of only a few bird families in which lunar synchrony in reproduction has been documented (Murton & Westwood 1977, Baker & Dekker 2000). Several studies note the influence of the moon on nightjar nesting behaviour (e.g. Jackson 1985, Mills 1986, Vilella 1995, Perrins & Crick 1996), particularly the benefits of provisioning newly-hatched young during periods of high moonlight.

The White-winged Nightjar *Caprimulgus candicans* is one of the rarest caprimulgids in the Americas, considered Endangered by BirdLife International (2000). Until recently, its breeding biology remained almost entirely unknown, but research in Paraguay since the discovery of a population there in 1995 (Lowen *et al.* 1997) has clarified some aspects of the species' breeding behaviour. The nest site, eggs and chick were documented for the first time after the discovery of a nesting female in 1997 (Capper *et al.* 2000, Clay *et al.* in prep.), and the nuptial display behaviour of the male was also described by Clay *et al.* (2000). Male nightjars perform ritualised display flights at small arenas – low anthills or termite mounds – located on the upper slopes of ridgelines in areas of open grassland. Although males were present on their display territories throughout the night, display activity was highest under cloudless conditions on moonlit nights. Display flights were accompanied by a dull “tk...grrrrt” noise of postulated mechanical origin, perhaps produced by movement of air through the outer primaries of the wing. A recording of this noise was released as part of Ranft & Cleere (1998).

Based on the clustering of male display territories they observed at Aguará Ñu, Clay *et al.* (2000) suggested that the Paraguayan population of White-winged Nightjars might exhibit a lek or ‘landmark’ mating system. Leks can be broadly defined as any aggregation of males visited by females primarily for the purposes of fertilisation (Höglund and Alatalo 1995). Four criteria were proposed by Bradbury (1981) to distinguish ‘classical’ leks from other lek-like mating systems: (1) lack of male parental care; (2) aggregation of males at an arena to which females come for mating; (3) arenas containing no resources required by females (e.g. nest sites, food) except males themselves; and (4) free mate choice by females visiting an arena. Lekking has been suggested to occur in at least three other species of caprimulgid (see Holyoak 2001), though for one the evidence is sparse (Lyre-tailed Nightjar *Macropsalis lyra*; Hilty & Brown 1986). However, no nightjars featured on a list of 97 lek-mating bird species compiled by Höglund & Alatalo (1995).

In this chapter, I present the first comprehensive description of the breeding biology of the White-winged Nightjar, on the basis of data collected during a three-year study in Paraguay. Aspects of male display behaviour and the distribution of male display territories are quantified for the first time, and the nesting biology of the species is documented using data from multiple nesting attempts. These data and the observed division of parental duties between the sexes are used to critically assess whether the study population exhibits a polygynous or lekking mating system. The information obtained on the species' breeding ecology is compared with that available for related species, and implications for the species' conservation are highlighted.

METHODS

Fieldwork was conducted over three breeding seasons (from September to January) between October 1998 and January 2001 at Aguará Ñu in eastern Paraguay (see Chapter 1). For simplicity, breeding seasons are referred to by their principal year: e.g. the season running from September 2000 to January 2001 is termed the '2000 season'. Adult nightjars were captured, sexed and ringed following the methods outlined in Chapter 2, and lightweight radio-transmitters were attached to certain individuals, including all adult females (see Chapter 4 for full details of radio-telemetry methods).

Male display territories

In the current study, the term 'display territory' is used to refer to the small area in which a male nightjar conducted all of his display activity during the breeding season. This term was used to allow direct comparison with Clay *et al.* (2000), and makes no assumptions regarding defence or exclusivity (but see Chapter 4). Each display territory contained a primary 'display arena', at which the male conducted the majority of its display activity, and some also contained one or more 'secondary' arenas, which were used more sporadically and when the male was disturbed from its primary arena (Clay *et al.* 2000). For the purposes of this chapter, the location of each display territory was defined by its primary display arena. Occasionally, the primary arena of a display territory changed between or, more rarely, within seasons. In such cases, the display arena that was utilised for longer was chosen for subsequent analyses. More comprehensive estimates of the size and configuration of male breeding ranges are provided in Chapter 4.

The study site was surveyed for displaying males each season between August and December. Males were initially located by the characteristic "tk...grrrrt" noise produced during display flights, which was audible from distances of up to *c.* 200 m under ideal conditions. Surveys were conducted on still, moonlit nights, when male display activity was at its highest (Clay *et al.* 2000, see also Results). No searches were carried out on nights with precipitation or strong wind (in excess of Beaufort force *c.* 5). Once a displaying male was detected, it was observed for 10-15

min to identify its primary display arena, the precise location of which was recorded using a Magellan 2000 XL GPS receiver. Each male was then captured and individually marked (Chapter 2). Male display territories were subsequently revisited on multiple occasions to conduct focal observations of male display behaviour. During these visits, the identity of the territory-holding male and the location of the primary (and any secondary) display arenas were confirmed.

To investigate whether displaying males showed any signs of large-scale aggregation, nearest-neighbour analysis (Clark & Evans 1954, Krebs 1989) was used to inspect the spatial distribution of display territories (see also Höglund & Stöhr 1997). The distance from each primary arena to its nearest neighbour was derived from GPS locations, and the average nearest-neighbour distance (NND) within each season was calculated. The method outlined by Clark & Evans (1954) was then used to obtain estimates of expected NND, assuming a random distribution of males within the survey area. The latter was defined by a convex polygon (of *c.* 400 ha) encompassing the zone that was surveyed most thoroughly for display territories (see Results). Since the small sample sizes in the current study prevented the use of a boundary strip, estimates of expected NND were corrected using Donnelly's (1978) adjustment for edge-effect bias. An index of aggregation (R) was obtained for each season by dividing the mean observed NND by the mean expected NND. When $R = 1.0$ the observed spatial distribution does not deviate from random, whereas values of R between 1 and 0 indicate an increasing degree of clustering (Krebs 1989).

The gross topographical characteristics of display territories and an equal number of random points were measured using a digital version of a 1:50,000 Paraguayan Instituto Geográfico Militar map, imported as a layer into a geographical information system (GIS) in ArcView 3.2 (ESRI 1999). Random sites were selected using grid references derived from a list of random numbers. The following variables were recorded for each site: (i) *gradient*, to the nearest 1°; (ii) *altitude*, to the nearest 5 m above sea level; (iii) *altitude difference*, from the nearest 'spot height' (peak local altitude); (iv) *distance to spot height*, to the nearest 25 m; (v) *distance to stream*, to the nearest 25 m; (vi) *aspect*, allocated to one of four quadrants (north-east, south-east, south-west and north-west).

Qualitative observations suggested that males did not select display arenas at random, even within display territories. To determine how display arenas differed from the population of available mounds, the structural characteristics of nine display arenas used during the 2000 season were measured and compared to those from a sample of random mounds. The arenas included the primary arenas of seven males, as well as two secondary arenas used on a regular basis. The following variables were measured for each mound: (i) *maximum height*, to the nearest 5 cm; (ii) *modal height*, i.e. height of the majority of the mound (excluding any 'towers'), to the nearest

5 cm; (iii) *basal 'circumference'*, to the nearest 0.1 m; (iv) *maximum basal chord*, across the longest axis of the mound, to nearest 0.1 m; (v) *presence/absence of 'towers'*, i.e. free-standing vertical structures projecting above the modal level of the mound (see Plate 3.1). At each display arena, four random mounds were selected by walking 20 m from the display arena on each of the four cardinal points of the compass, and then identifying the nearest mound. On two occasions it was not possible to locate a mound: the total number of random mounds measured was 34.

Male display behaviour

To collect quantitative and qualitative data on male display behaviour, 30-minute focal watches were conducted at the primary display arenas of territory-holding males. Focal males were monitored from *c.* 10-20 m away with the aid of a torch set on diffuse beam. Individuals did not appear unduly disturbed by the presence of the observer, and on other occasions continued to display with an observer just 5 m away. For the purposes of this study, nautical twilight (the time at which the sun is 12° below the horizon) was used as the point delineating dusk or dawn from true 'night' (Brigham & Barclay 1992). Until this point, any illumination from the moon is greatly exceeded by the remaining scattered light from the sun (Austin *et al.* 1976). Seventy-one percent (64 of 90) of focal watches were begun before the end of nautical twilight, and thus termed 'dusk watches'. The remaining 26 watches were conducted under truly nocturnal conditions and termed 'night watches'. Watches were not conducted under conditions of precipitation or strong wind (in excess of Beaufort force *c.* 5).

During dusk watches, the observer was present at the observation point from shortly after sunset, and the watch commenced when the focal male arrived at the display arena. To allow for any disturbance resulting from the arrival of the observer, a five minute 'settling' period was allowed prior to starting night watches. Once the focal watch had started, the number and time of all displays were recorded, as well as details of any interactions with other individuals. For the purposes of this study, a 'display' was defined as any flight up from the display mound accompanied by both the "tk" and "grrrrt" sounds. Following the completion of the watch, the identity of the focal male was confirmed by inspecting its colour rings and unique reflective tail mark (Chapter 2).

Potential environmental correlates of male display rate were investigated using a multiple regression model. The following variables were entered into the model: (i) *time*, in minutes since the end of nautical twilight; (ii) *temperature*, minimum recorded during the watch; (iii) *moon phase*, proportion of the moon face illuminated, MFI; (iv) *moon height*, estimated angle above the horizon in degrees; (v) *moonlight*, estimated lunar illuminance. Ambient temperature was measured every 15 min using an electronic Tinytag logger (www.geminidataloggers.com), which was

programmed to record the minimum air temperature to the nearest 0.1° C. Details of astronomical phenomena (i.e. MFI, times of sunrise/sunset, moonrise/moonset and twilights) were obtained from tables in the *Astronomical Almanacs* for the years 1998 to 2001. A number of factors influence overall lunar illuminance, two of the most important being the phase of the moon and its angle above the horizon (Austin *et al.* 1976). However, neither factor shows a simple linear relationship with illuminance (R. Willstrop *in litt.* 2001), so their combined effects were estimated, using the information provided in Austin *et al.* (1976), and included as a separate measure: ‘moonlight’.

Tape recordings of the male display noise and other ‘vocalisations’ were obtained using a directional MKH416T Sennheiser microphone and a WM-D6C Sony Professional Walkman. Recordings were made at the display arenas of marked males, from distances of *c.* 5-10 m, during the 1999 and 2000 breeding seasons. Recordings were later digitised using the software package Avisoft-SASLab Pro, a 16-bit acquisition card and a sampling frequency of 4,000-22,050 Hz, depending on the maximum frequency of each vocalisation. Spectrograms of the male display noise were generated in Avisoft using the following settings: FFT-length = 128; frame size = 100%; window = Blackman; overlap = 75%. These settings provided sufficiently fine temporal resolution (8 ms) for the separate elements of the “grrrrrt” noise to be distinguishable. The following temporal measures were obtained using the on-screen cursors (Figure 3.1): interval between the “tk” and “grrrrrt” components (INT); length of the “grrrrrt” component (GTLEN); number of elements making up the “grrrrrt” (GTNUM). Frequency measures were not taken, however, given the relatively poor resolution (31 Hz) and limited frequency range of display noises.

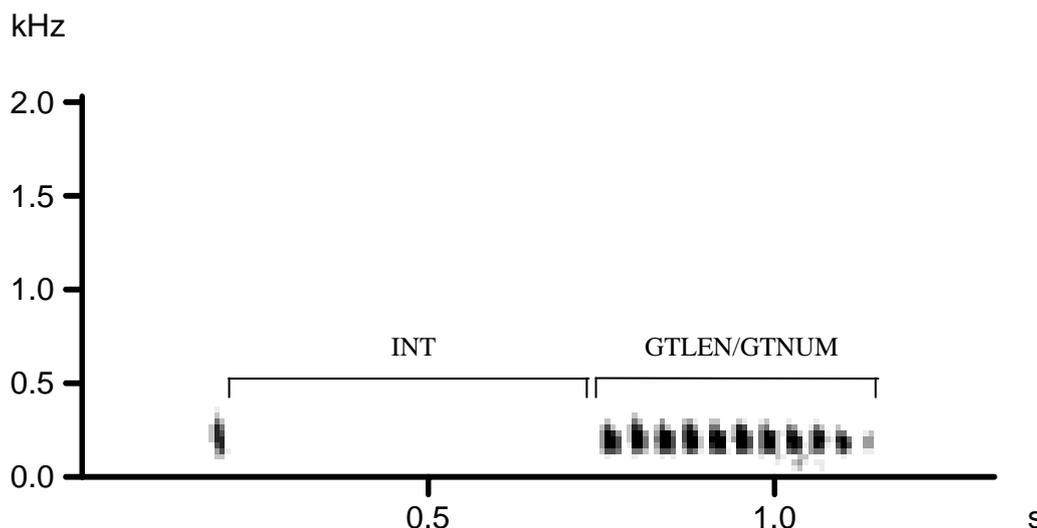


Figure 3.1 Spectrogram of male display noise showing “tk” and “grrrrrt” components and the three temporal variables measured for each recording (see text for definitions).

Nesting biology

Nest sites were located by monitoring radio-tagged females and checking their daytime 'roosts' for eggs every *c.* 2 days during the breeding season. The 'initiation date' for a nesting attempt was defined as the date on which the first egg was laid: the presence of eggs was the only factor that reliably distinguished nest sites from roost sites. Once a nest was initiated, its precise location was recorded using a GPS receiver. Gross topographical characteristics of nest sites and an equal number of random sites were measured as described above for male display territories. To ensure that random sites reflected those available to, but not used by, nesting females, they were selected to fall within 400 metres of the nest sites with which they were paired. Two radio-tagged females monitored during the 2000 breeding season ranged up to 403 ± 33 m from the centre of their breeding ranges (see Chapter 4). The following variables were recorded for each site: (i) *gradient*, to the nearest 1°; (ii) *altitude*, to the nearest 5 m above sea level; (iii) *distance to nearest stream*, to the nearest 25 m; (iv) *distance to nearest male display arena*, to the nearest 10 m; (v) *aspect*, allocated to one of four quadrants (north-east, south-east, south-west and north-west); (vi) *habitat*, classified as one of two dominant types (campo cerrado and wet grassland). Habitat type was determined from a simplified habitat map of the study site, added as a layer to the GIS (see Chapter 4).

The mass of freshly-laid eggs was measured to the nearest 0.5 g using a 100 g Pesola balance. Measures of the length and maximum breadth of eggs were taken to the nearest 0.1 mm using dial callipers. Egg volume was estimated using the equation: $\text{volume} = 0.51 * \text{length} * (\text{maximum breadth})^2$, following Hoyt (1979). During the egg stage, nests were visited every three to five days to confirm the sex of any adults present. These 'spot-checks' were carried out at various times of the day and night, and were independent of ongoing radio-telemetry fixes taken to characterise the home range and movements of individuals (see Chapter 4). Although radio-tracking equipment was sometimes used to confirm the identity of an adult, the bird's location was not known prior to any spot-check.

Hatching success was calculated as the percentage of eggs laid that hatched successfully. This method can produce biased (typically artificially high) values for hatching success, as it does not take into account nests failing before they are found (Beintema & Müskens 1987). However, the method of nest location used in the current study reduced this risk, and the data were adjudged insufficient to justify the use of the daily exposure method of Mayfield (1961, 1975). Nests were visited every two to four days after hatching, and chicks were weighed (to the nearest 0.5 g) using a 100 g Pesola balance, to obtain data on their growth and development. Chicks were ringed when they were *c.* 10 days old, by which time their tarsus width was already comparable to that of adult birds. Younger chicks were individually marked with non-toxic, white correction fluid on their feet.

During the nestling period, nocturnal focal watches of 50-255 min were conducted at nests to characterise the distribution of chick brooding and provisioning duties by the parents. Nest sites were monitored from *c.* 10-20 m away, using a head torch on diffuse beam to obtain eye shine from visiting adults without disturbing them. The duration (to the nearest five seconds) of each nest visit was recorded, as well as the sex of the visiting adult. Radio-tracking equipment was occasionally used to confirm the identity of tagged birds, but monitoring was conducted primarily on a visual basis. The data collected were used to calculate mean visit rates and average times spent at, or away from, the nest site. A small number of daytime spot-checks were also conducted to document the parental allocation of diurnal brooding duties.

Chick paternity

The paternity of nightjar chicks was investigated using the amplified fragment length polymorphism (AFLP) technique developed by Vos *et al.* (1995). This technique generates highly reproducible fingerprints for DNA of any origin or complexity, and requires no prior knowledge of DNA sequences for the development of suitable primers. The procedure is based on the selective polymerase chain reaction (PCR) amplification of restriction fragments resulting from a total digest of genomic DNA. When these fragments are separated and visualised by gel electrophoresis, the resulting multi-locus fingerprint patterns can be interpreted for paternity analyses. Although there are still relatively few published studies involving the use of AFLPs (Gerber *et al.* 2000), the technique has been used for paternity analysis in both plant and bird species (Krauss 1999, Questiau *et al.* 1999).

Full details of the methods used to assess chick paternity using the AFLP technique will be provided elsewhere (Dasmahapatra *et al.* in prep.). Blood samples were obtained from chicks *c.* 15 days after hatching by clipping a toenail, and from the brachial vein of adults during normal capture procedures (see Chapter 2). All samples were stored in 95% ethanol until DNA extraction. Seven primer pairs were used for the selective amplification of restriction fragments, and the resulting AFLP profiles were scored manually for the presence and absence of polymorphic loci. AFLP markers show dominant-recessive inheritance, and so the presence of a band in a chick profile must be explained by its presence in at least one of the parent profiles. In this study, the identity of the most probable set of parents for each chick was determined by inspecting a matrix of total 'band discrepancies' between the chick profile and each potential combination of parents. The band discrepancy for the correct parental pair should be zero, but slightly more conservative criteria are usually employed, to allow for mutations or scoring errors (Krauss 1999, Questiau *et al.* 1999). In practice, parental combinations were excluded in the current study if they failed to explain three or more markers in the chick profile.

Statistical analysis

All data were tested for normality and homoscedasticity prior to analysis using standard parametric and non-parametric univariate tests. If appropriate, data were subsequently analysed using multivariate techniques. When the dependent variable was continuous (e.g. male display rate), multiple linear regression was used to investigate the effects of potential covariates. Analyses were conducted using a forward stepwise procedure with entry and removal probabilities set at $P = 0.05$. At each step, the variable with the most significant score statistic was entered into the model, providing that its inclusion significantly improved the fit of the model: significance was tested using partial F -tests (Hair *et al.* 1995). This process was repeated until no further variables met the criteria for entry or removal, at which point the model was considered to be final.

When the dependent variable could be allocated to one of two discrete categories (e.g. display territory or random site, display mound or random mound), binary logistic regression was used to identify which combination of variables best distinguished between the two categories. Analyses were conducted using a forward stepwise procedure as outlined above, but with significance tested using likelihood ratio tests in which the difference in deviance ($-2 * \log_e$ likelihood) between models with and without the variable was treated as χ^2 , with degrees of freedom equal to the number of parameters being added (Manly *et al.* 1993). When comparing display mounds and random mounds, the inclusion of secondary mounds for two males raised the issue of potential bias resulting from pseudoreplication. To address this, the parameter estimates produced by the model were jack-knifed following the procedure detailed in Sokal & Rohlf (1995), taking the male as the sampling unit. In practice, the jack-knifed parameter estimates did not differ significantly from those produced by the original model, suggesting that pseudoreplication was not a major problem.

Categorical data were analysed using the G -test of independence. A form of the G -test for goodness of fit, adjusted using the William's correction for the two-cell case (Sokal & Rohlf 1995), was used to compare the observed sex ratio of adult captures with that expected on the basis of a 1:1 sex ratio. In all cases, statistical significance was set at $P < 0.05$ unless otherwise specified, and means are given \pm one standard error.

RESULTS

Forty-nine nightjars (34 adult and 15 young birds; Table 3.1) were captured and ringed between 1998 and 2001. The sex ratio of captured adults was biased towards males in all three field seasons, and the overall ratio of 3.25 males to 1 female differed significantly from parity. The four females captured in 1998 were all caught late in the breeding season, and none of them was subsequently confirmed to (re-)nest that season; two individuals captured in late-December had already begun post-nuptial flight feather moult (see Chapter 2). Hence, all data on nesting biology were obtained from females captured during the 1999 and 2000 breeding seasons.

Table 3.1 Sex and age composition of nightjar captures by season.

Season	Males	Females	Young birds	Total	Sex ratio (males/female)	<i>G</i>	<i>P</i>
1998	20	4	3	27	5.00	11.41	< 0.001
1999	14	3	5	22	4.67	7.50	< 0.01
2000	9	3	9	21	3.00	3.01	NS
Overall ^a	26	8	15	49	3.25	9.89	< 0.005

^a Column totals do not equal 'Overall' total due to recapture of certain individuals between seasons.

Male display territories

Display territories were identified for ten males in 1998 and eight males in each of 1999 and 2000. One territory, discovered late in the 2000 breeding season, was excluded from the nearest-neighbour analysis as it was located outside the normal survey area (Figure 3.2). The remaining territory-holding males occurred at a mean density of one male per 50 ± 5 ha ($n = 3$ seasons) within the area surveyed. The closest male display territories were just 70 m apart (in 1998), but the average nearest-neighbour distance across all three seasons was 254 ± 8 m. Aggregation indices confirmed that display territories were significantly clustered within the survey area in all three seasons (Table 3.2).

Table 3.2 Mean \pm se nearest-neighbour distances (NND) and degree of aggregation for male display territories during three breeding seasons.

Season	No. display territories	Observed NND (m)	Expected NND (m) ^a	Aggregation index (<i>R</i>)	Significance ^b
1998	10	253 ± 97	372 ± 69	0.68	$z = -1.71, P = 0.044$
1999	8	241 ± 35	425 ± 89	0.57	$z = -2.07, P = 0.019$
2000	7	268 ± 34	460 ± 103	0.58	$z = -1.87, P = 0.031$

^a Assuming random distribution of males within 406 ha survey area (see Methods).

^b *P*-values from one-tailed *z*-tests (Campbell 1996).

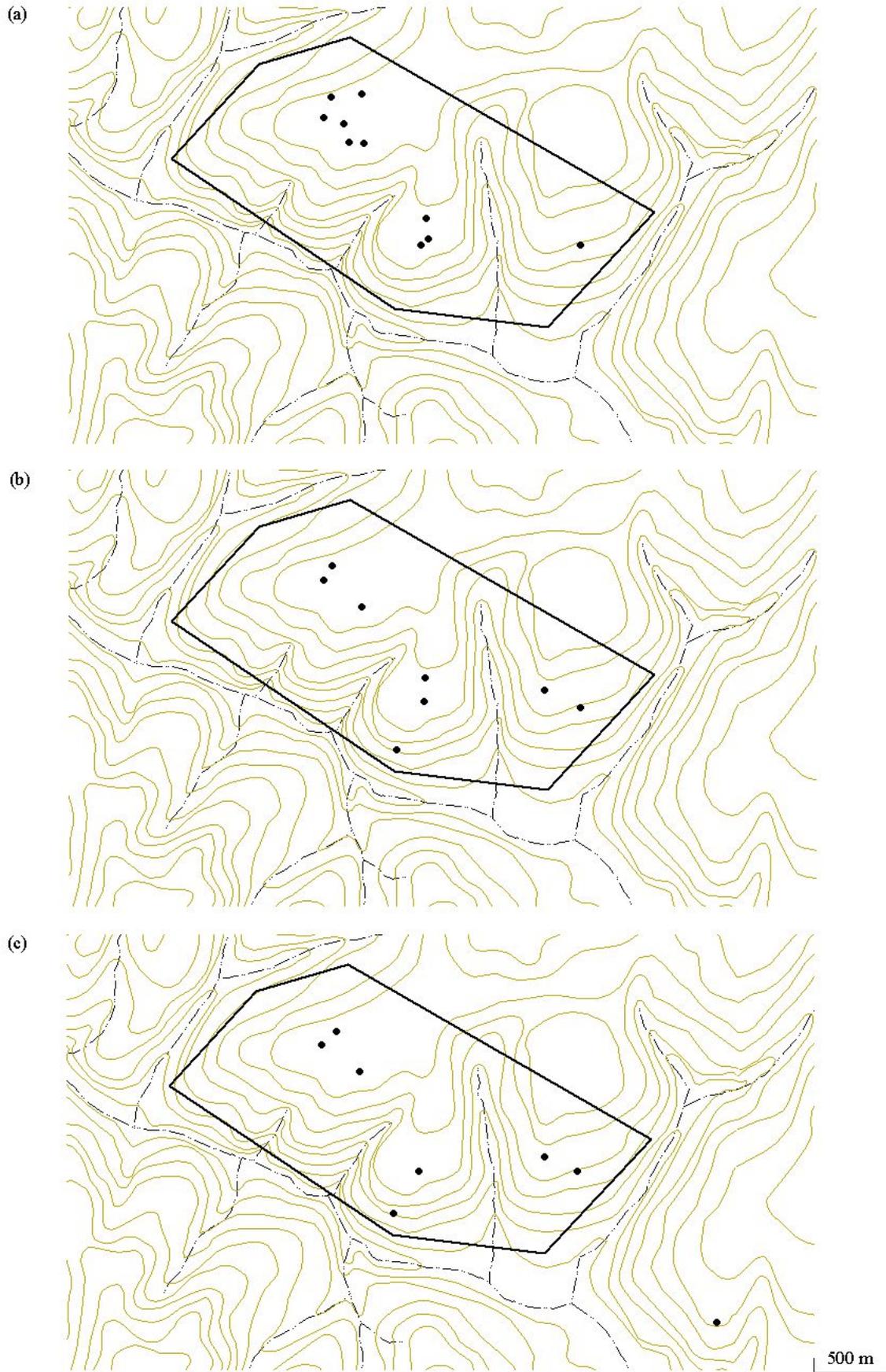


Figure 3.2 Location of male display territories (closed circles) during: (a) 1998; (b) 1999; and (c) 2000 breeding seasons. Pale grey lines are contours, dashed lines are watercourses. The polygon represents the *c.* 400-ha survey area.

In total, 13 distinct display territories were identified between 1998 and 2000: five of these were occupied in all three breeding seasons, and a further three were occupied in at least two. The ownership of certain display territories changed both between and, less frequently, within seasons, but these changes were almost certainly due to the death or emigration of the original territory-holding male. Following nine such changes in territory ownership, the original male was never recorded again. In the remaining two instances, the male was found to have moved to a display territory vacated by another ‘missing’ male.

Inspecting the distribution of display territories indicated that they were located almost exclusively on the upper slopes of ridgelines running perpendicular to the main Arroyo Guyrá Kehá valley (running north-west to south-east across the lower half of the maps in Figure 3.2). Preliminary analysis of gross topographical characteristics using univariate tests suggested that display territories differed significantly from random points for only one variable (Table 3.3). A binary logistic regression model, explaining *c.* 27% of the deviance in site use, also revealed ‘distance to stream’ to be the only significant predictor (Table 3.4): on average, display territories were further from streams than random points. The model correctly reclassified 69% of sites overall, with an equal degree of reclassification success for display territories and random sites. Aspect was not entered into the model, but univariate tests suggested that territories were more likely to have a westerly than easterly aspect compared to random points (11 of 13 *versus* 5 of 13; *G*-test: $G = 5.80$, $df = 1$, $P < 0.05$).

Table 3.3 Mean \pm se values of topographical variables for male display territories used during 1998-2000 and an equal number of random points.

Variable	Display territories ($n = 13$)	Random points ($n = 13$)	Significance ^a
Gradient (°)	2.2 \pm 0.6	4.5 \pm 0.7	$W = 220$, $P = 0.023$
Altitude (m)	232 \pm 4	214 \pm 6	$t_{24} = -2.51$, $P = 0.019$
Altitude difference (m)	11 \pm 3	29 \pm 7	$W = 220$, $P = 0.023$
Distance to spot height (m)	406 \pm 77	683 \pm 110	$t_{24} = 2.06$, $P = 0.050$
Distance to stream (m)	567 \pm 74	310 \pm 46	$W = 122$, $P = \underline{0.007}$
Aspect – number of sites facing:			
NE (0-90°)	0 (0%)	0 (0%)	
SE (90-180°)	2 (15%)	8 (62%)	
SW (180-270°)	6 (46%)	2 (15%)	
NW (270-360°)	5 (38%)	3 (23%)	

^a From unpaired *t*-tests or Mann-Whitney *U*-tests. Values underlined indicate table-wide significance at an adjusted initial α level of 0.01 (Rice 1989).

Table 3.4 Summary of the model discriminating between male display territories ($n = 13$) and an equal number of random points.

Variable	Coefficient	SE	% correctly reclassified ^a	% of deviance explained ^b	χ^2	df	P
Intercept	-3.543	1.617					
Distance to stream	0.009	0.004	69.2	27.4	9.89	1	< 0.005

^a Percentage of points correctly reclassified by the model as display territories ($P > 0.5$) or random ($P < 0.5$).

^b Total deviance = 36.0; residual deviance = 26.2.

At a finer scale, preliminary analysis of the structural characteristics of mounds used as display arenas in 2000 suggested that they differed significantly from random mounds for a number of variables (Table 3.5). However, a binary logistic regression model, explaining 25% of the deviance in mound use, showed ‘modal height’ to be the only significant predictor (Table 3.6): on average, display mounds were lower than random mounds. The model correctly reclassified 91% of random mounds, but only 22% of mounds used as display arenas, resulting in an overall correct reclassification rate of 77%.

Table 3.5 Mean \pm se values of the structural characteristics of male display arenas used during 2000 breeding season compared to a sample of random mounds.

Variable	Display arenas ($n = 9$)	Random mounds ($n = 34$)	Significance ^a
Maximum height (m)	0.42 \pm 0.10	0.61 \pm 0.04	$W = 831, P = 0.014$
Modal height (m)	0.24 \pm 0.03	0.51 \pm 0.05	$W = 842, P = \underline{0.006}$
Basal ‘circumference’ (m)	6.0 \pm 0.8	3.7 \pm 0.5	$W = 665, P = \underline{0.013}$
Maximum basal chord (m)	2.1 \pm 0.3	1.1 \pm 0.1	$W = 654, P = \underline{0.005}$
‘Tower(s)’:			
<i>present</i>	3 (33%)	8 (24%)	$G = 0.32, NS$
<i>absent</i>	6 (67%)	26 (76%)	

^a From Mann-Whitney U -tests or G -test. Values underlined indicate table-wide significance at an adjusted initial α level of 0.01 (Rice 1989).

Table 3.6 Summary of the model discriminating between male display arenas used during the 2000 breeding season ($n = 9$) and a sample of random mounds ($n = 34$).

Variable	Coefficient	SE	% correctly reclassified ^a	% of deviance explained ^b	χ^2	df	P
Intercept	1.432	1.049					
Modal height	-8.236	3.551	76.7	25.0	11.01	1	< 0.001

^a Percentage of mounds correctly reclassified by the model as display arenas ($P > 0.5$) or random ($P < 0.5$).

^b Total deviance = 44.1; residual deviance = 33.1.

Male display behaviour

In both 1999 and 2000, sporadic display activity was noted on certain nights in the lead up to the August full moon, but male display activity did not commence in earnest until September. Activity levels remained high through October to December, but had subsided by early January: the latest date on which display activity was noted was 6 January (in 2000). Hence, the overall period of male display activity broadly coincided with the vocal activity of other nightjar species breeding at the study site (Figure 3.3).

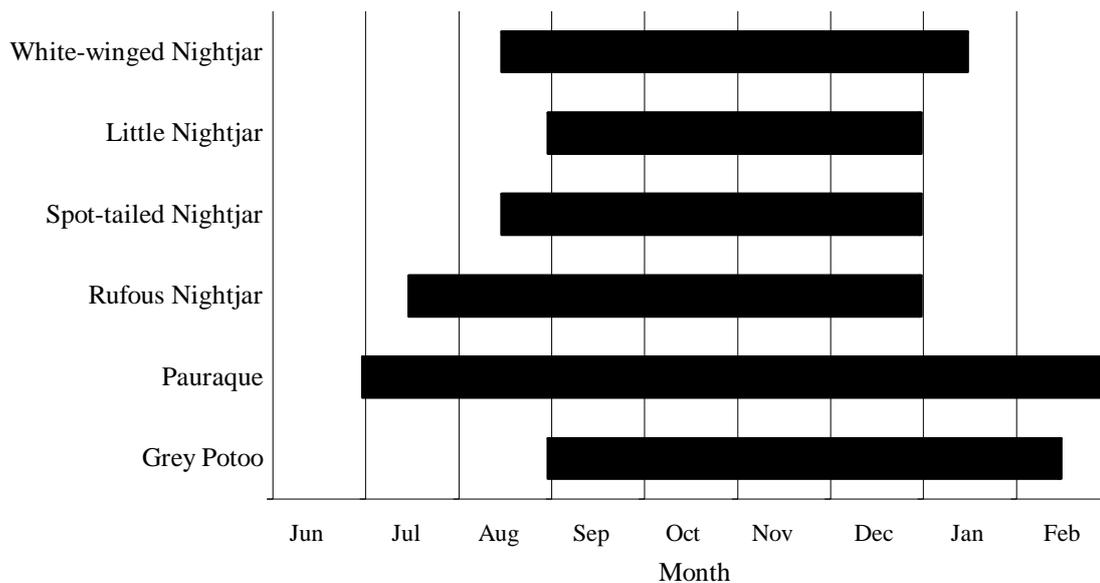


Figure 3.3 Timing of White-winged Nightjar display activity in comparison to vocal activity of other nightjar (and one potoo) species breeding at Aguará Ñu.

Although an attenuated version of the mechanical “grrrrrt” sound was occasionally heard at the start of foraging sallies, the full “tk... grrrrrt” display noise was only ever observed in the context of male display flights at arenas. These display flights were more variable than those described by Clay *et al.* (2000). The majority (63%) were initiated from a display perch, but 23% immediately followed the return of the male from a foraging sally, and the remaining 14% involved males already present on their display arena ($n = 132$ displays by five males in 2000). In the latter case, the male was observed to jump on the display arena to produce the “tk”, before flying up with the “grrrrrt” noise as per usual. Observations from the current study showed that display activity was not solely restricted to males in definitive plumage (see Chapter 2). A pre-definitive male, approximately mid-way through moulting into the definitive white plumage (i.e. retaining five or six juvenile outer primaries), was observed to display on two nights in early November 1998 (see below).

Recordings of 8-19 display noises were obtained for eight marked males during the 1999 and 2000 breeding seasons. Spectrograms showed that display noises had a relatively fixed structure, with the “tk” and “grrrrt” components separated by 500 to 700 ms, but with broadly similar frequency ranges (*c.* 100-400 Hz; see Figure 3.1). The display noises produced by the pre-definitive male in 1998 were of a noticeably higher frequency, but unfortunately it was not possible to obtain a recording of its display for direct comparison. Two of the three temporal measures (GTLEN and GTNUM) were highly correlated (Spearman rank correlation: $r_s = 0.96$; $n = 103$; $P < 0.001$). Only GTNUM was considered further, as it was adjudged less likely to be subject to measurement error. Males showed significantly more inter- than intra-individual variation for both INT (Kruskal-Wallis test: $H = 57.82$, $df = 7$, $P < 0.001$) and GTNUM ($H = 60.40$, $df = 7$, $P < 0.001$), suggesting consistent inter-individual differences in these temporal measures.

A total of 90 focal watches was conducted at male display arenas over the course of three breeding seasons (1998: $n = 10$; 1999: $n = 20$; 2000: $n = 60$). No significant differences in display rate were apparent between seasons (Kruskal-Wallis test: $H = 1.18$, $df = 2$, $P > 0.05$), so data were pooled for subsequent analyses. On average, males performed 0.54 ± 0.04 displays per minute during focal watches, although considerable variation in display rate was apparent (range: 0.00-1.37 displays/min; $n = 90$). However, when comparing the six males for which five or more focal watches were conducted, no evidence was found to suggest that this variation was due to consistent inter-male differences in display rate ($H = 5.95$, $df = 5$, $P > 0.05$).

Observations from dusk watches showed that, on average, males arrived at their display arenas 26.6 ± 0.6 minutes after sunset and 27.9 ± 0.7 minutes before the end of nautical twilight. Upon arrival, males showed a burst of high display activity. The mean display rate in the first half of dusk watches was more than twice that in the second half (0.75 ± 0.06 versus 0.35 ± 0.04 displays/min; Wilcoxon signed ranks test: $T = 1742$, $n = 64$, $P < 0.001$), whereas there was no significant difference between the two halves of night watches (0.50 ± 0.07 versus 0.54 ± 0.06 displays/min; paired t -test: $t_{25} = -1.01$, $P > 0.05$). When considering night watches alone, ‘moonlight’ was the only environmental variable capable of explaining a significant amount of the variation observed in display rate (overall fit of model: $R^2 = 0.166$, $F_{1,24} = 4.77$, $P < 0.05$). Display rate showed a positive relationship with this estimate of overall lunar illuminance, reflecting a tendency for males to display more when the moon was fuller and higher in the sky (Figure 3.4). Nevertheless, even when conditions were not suitable for display activity, males were generally still present – either sallying or resting – on their display territories. There was no significant relationship between display rate and sallying rate during focal watches in which the latter was measured (Spearman rank correlation: $r_s = -0.26$; $n = 36$; $P > 0.05$)

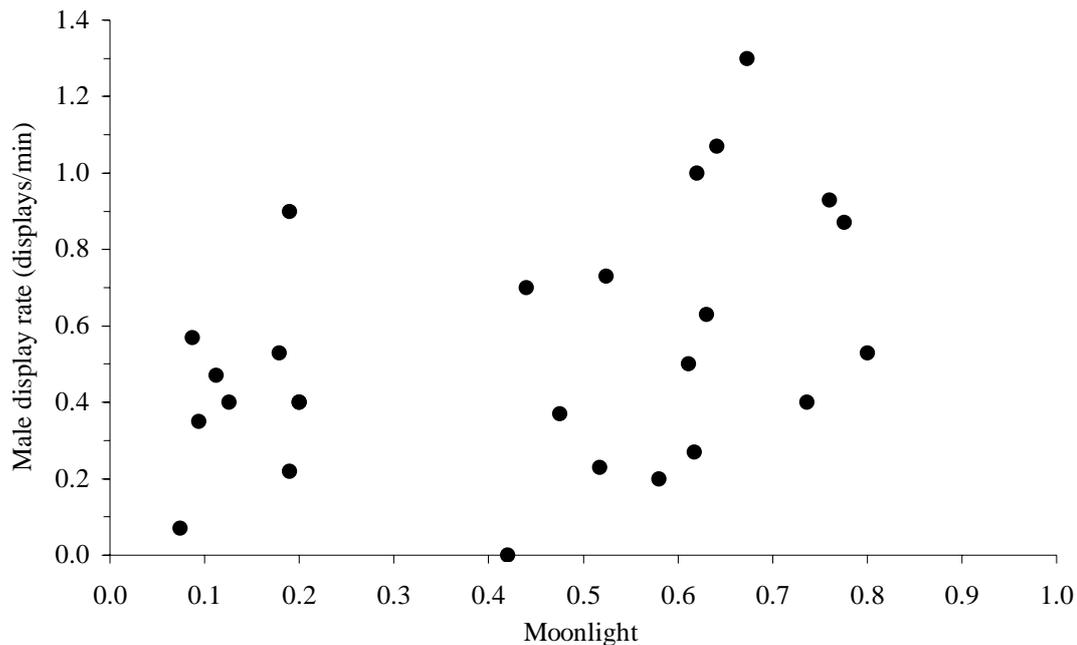


Figure 3.4 Male display rate in relation to ‘moonlight’, an estimate of lunar illuminance (see Methods). Data from ‘night’ watches only (Pearson correlation: $r = 0.41$, $n = 26$, $P < 0.05$).

During one display watch in November 1998, the focal male produced a previously undocumented, insect-like “tik tik” call whilst perched in the vicinity of its display arena. This vocalisation (or a single “tik” equivalent) was subsequently recorded on several occasions during display watches (see Figure 3.5 for spectrogram of call), and was only ever produced by males perched in or near their display arena. The thin, high-pitched nature of the call made it difficult to detect under certain conditions, but it was apparently produced at rates of 1.24 ± 0.20 “tik tiks” per minute (range: 0.00–3.33 calls/min; data from 26 display watches). There was no significant correlation between the rate of “tik tik” production and male display rate during display watches (Pearson correlation: $r = 0.31$, $n = 26$, $P > 0.05$).

Aggressive interactions between males were observed during 14 focal watches (30% of watches for which details were noted), and on various occasions during *ad hoc* observations at display arenas. Interactions typically comprised rapid chases, sometimes involving up to three males, and occasionally also physical contact. A soft, liquid ‘gurgling’ call produced during chases was noted on a number of such occasions. Aggressive interactions were observed most frequently at one particular display arena (‘PLA1’; 11 of 14 watches), and this bias was significant when allowing for the distribution of watches among display arenas (G -test: $G = 7.64$, $df = 1$, $P < 0.01$). There was a non-significant trend for higher rates of display activity during watches that included male-male chases compared to during those that did not (0.74 ± 0.10 versus 0.53 ± 0.06 displays/min; unpaired t -test: $t_{44} = -1.76$, $P = 0.085$).

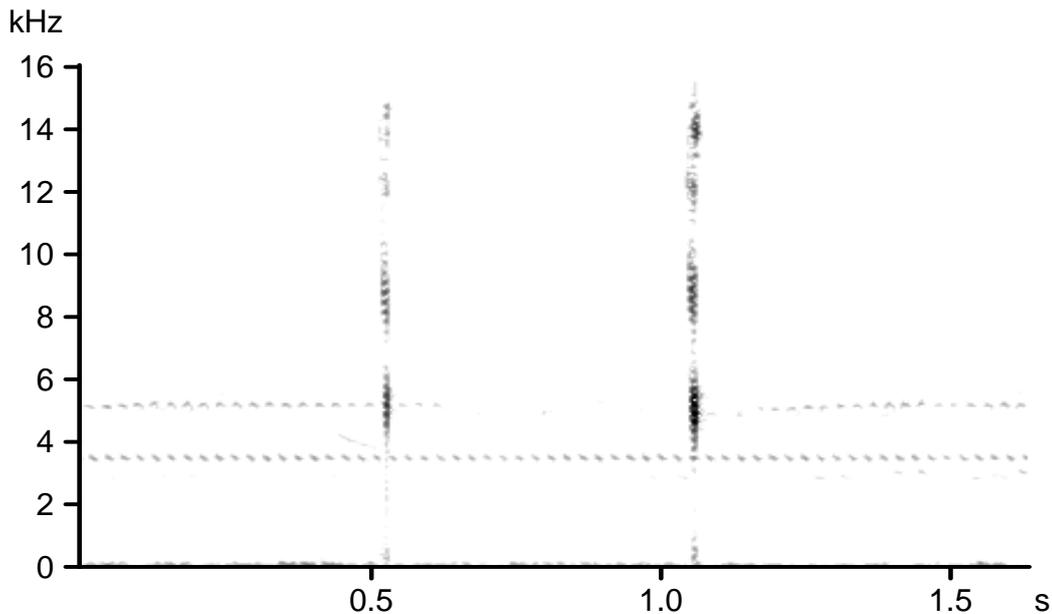


Figure 3.5 Spectrogram of previously undescribed, insect-like “tik tik” call given by male nightjars when inactive in vicinity of display arenas. Note background insect noise at *c.* 3.5 and 5.0 kHz. Recordings made by M. C. Velázquez at Aguará Ñu in December 2000.

It was not possible to record female visits to male display arenas reliably, due to difficulties in distinguishing unmarked females from juveniles, or from females of other similarly-sized species (e.g. Little Nightjar *Caprimulgus parvulus*). However, during one dusk watch in October 1998, five nights prior to full moon, a female visit and presumed copulation were documented. Over the course of *c.* 20 min, the female landed on the display arena at least twice, and three presumed copulation attempts by the focal male were witnessed. Prior to one attempt, the male appeared to display to the female whilst they were both perched on the arena, by spreading its wings and cocking and splaying its tail. When the female left the display arena after copulation, the male followed and flew parallel to her with wings raised and a slow buoyant flight, conspicuously different to the rapid flight typical of male-male encounters. On another occasion, in December 2000, a male was observed to conduct a similar ‘escort’ flight, with raised wings, for a presumed female flying through his display territory.

Nesting biology

Nine breeding attempts by four different females were documented during this study: five in 1999 and four in 2000 (Table 3.7). A fifth female captured in early December 2000 was heavily gravid, but she was never subsequently relocated. As with most nightjar species, female White-winged Nightjars did not construct a nest. Eggs were laid directly on the ground, in a small ‘tunnel’ between tussocks of grass or herbaceous plants and facing onto a small area of bare earth (*c.* 25-50 cm in diameter). As at roost sites (see Chapter 4), the latter apparently served as a ‘runway’ for the

Table 3.7 Summary of nesting attempts observed during 1999 and 2000 breeding seasons.

Season	Female	First nesting attempt				Second nesting attempt			
		Date first egg laid	Incubation period	Hatching date	Chicks last seen at nest site	Date first egg laid	Incubation period	Hatching date	Chicks last seen at nest site
1999	F063	26 September	— ^a	—	—	25 October	19 days	13 November	1 December ^{b†}
1999	F066	25 September	19 days	14 October	25 October ^{c†}	21 November	19 days	10 December	14 December ^d
1999	F067	—	—	—	—	—	—	— ^e	10 December [†]
2000	F010	—	—	— ^f	18 October ^{g†}	12 November	19 days	1 December	14 December [†]
2000	F066	11 October	17 days	28 October	— ^h	13 November	19 days	2 December	17 December [†]

^a Eggs depredated by unknown predator within one week of laying.

^b Smaller of two chicks disappeared during afternoon of 28 November; larger chick no longer present by 3 December.

^c Nest not checked for five days; no sign of chicks on 31 October.

^d Both chicks still present – no further fieldwork in 1999.

^e Single chick discovered on 23 November; estimated by mass and stage of feather development as approximately 10 days old.

^f Two chicks discovered on 13 October; estimated by mass and stage of feather development as approximately 10 days old.

^g Female and chicks found to have moved to new site by 20 October; not seen subsequently.

^h Chicks disappeared, presumably depredated, within one week of hatching.

[†] Denotes chick(s) believed to have fledged successfully.

adult bird. There was no evidence to suggest that the gross topographical characteristics of nest sites differed significantly from those of random sites available to nesting females (Table 3.8).

Table 3.8 Mean \pm se values of topographical variables for nest sites used in 1999 and 2000 and an equal number of random sites.

Variable	Nest sites (<i>n</i> = 9)	Random sites (<i>n</i> = 9)	Significance ^a
Gradient (°)	5.6 \pm 1.2	4.8 \pm 0.9	$t_{16} = -0.52$, NS
Altitude (m)	218 \pm 5	217 \pm 5	$t_{16} = -0.07$, NS
Distance to nearest stream (m)	306 \pm 61	319 \pm 54	$t_{16} = 0.17$, NS
Distance to nearest male display arena (m)	227 \pm 49	208 \pm 56	$t_{16} = -0.25$, NS
Aspect – number of sites facing:			
NE (0-90°)	1 (11%)	0 (0%)	
SE (90-180°)	1 (11%)	1 (11%)	
SW (180-270°)	5 (56%)	6 (67%)	
NW (270-360°)	2 (22%)	2 (22%)	
Habitat – number of sites in:			
Campo cerrado	6 (67%)	8 (89%)	
Wet grassland	3 (33%)	1 (11%)	

^a From unpaired *t*-tests.

The initiation date was confirmed for seven clutches, and consistently fell within two days of a full moon (1.3 ± 0.3 days; range: 0-2). The earliest initiation date observed was 25 September (in 1999), though two chicks discovered on 13 October 2000 were estimated to be approximately ten days old, and had probably hatched from eggs laid over the full moon of 14 September. Females made two nesting attempts per season, using a different site for each attempt (mean distance between nest sites: 360 ± 31 m; range: 296-461 m; *n* = 4). The female (F067) captured in late November 1998, whilst brooding a single chick, was almost certainly making a second breeding attempt (Table 3.7).

Clutch size was two for all seven clutches discovered at the egg stage. It was not possible to check each nest daily, but the second egg was generally laid within 24 hours of the first, though in one case there was a delay of at least 30 hours. Eggs were broadly similar to the description provided by Clay *et al.* (in prep.): pale cream-beige in colour, with a variable pattern of dark brown and mauve-grey speckling and blotching. Differences in egg patterning were observed within most clutches, with one egg more densely and uniformly covered in fine markings, and the other showing fewer, larger markings, often with a sub-apical ring of grey blotches at the obtuse pole (see Plate 3.2). A summary of the morphometrics for 14 eggs is provided in Table 3.9. The eggs of a clutch weighed on day 1 and again on day 18 of incubation had both decreased in mass by 0.7 g (11% and 12%) during the intervening period.

Table 3.9 Summary of morphometrics of 14 nightjar eggs from seven clutches.

Measure	Mean \pm se	Range
Mass (g) ^a	6.7 \pm 0.1	5.8-7.5
Length (mm)	27.7 \pm 0.3	26.7-29.9
Maximum breadth (mm)	21.0 \pm 0.1	19.8-21.7
Volume (cm ³)	6.2 \pm 0.1	5.4-7.1

^a Mass provided only for eggs weighed within two days of laying ($n = 10$)

Incubation began with the laying of the first egg, and was carried out exclusively by the female: on no occasion was the male found at the nest site. Thirty-four ‘spot-checks’ were conducted at seven nests during the incubation period, and the female was found to be in attendance during 100% (20 of 20) of diurnal and 57% (8 of 14) of nocturnal checks. On the remaining six occasions, the nest site and eggs were unattended. During nine daytime checks, the female was found to be incubating only one ($n = 3$) or neither ($n = 6$) of the two eggs. There was no significant difference in ambient air temperature on these occasions compared to 11 occasions when the female was incubating both eggs (unpaired t -test: 23.4 ± 1.8 °C versus 23.7 ± 1.3 °C; $t_{18} = -0.13$; $P > 0.05$). Although it was not possible to confirm the hatching date for every clutch, the modal incubation period was 19 days and chicks probably hatched within 24 hours of each other.

Hatching success was 86% (12 of 14 eggs) for the seven nests for which initial clutch size was known. At hatching, chicks had open eyes and were covered in a pale buff-coloured down, with greyish legs and a pale-tipped greyish bill. The average mass of four chicks (from two clutches) weighed on the day of hatching was 5.2 ± 0.1 g. The growth rates of eight chicks from four broods are presented in Figure 3.6. Clear asymmetry in growth rate was observed in two broods. In one brood (circular symbols in Figure 3.6), the mass of the larger chick (26.3 g) was already more than twice that of its sibling (10.9 g) by day 10. The ‘runt’ disappeared, presumably dead, by day 15.

Nocturnal focal watches conducted at six nests (of four females) showed chick brooding and provisioning duties to be undertaken solely by the female. Over the course of almost 25 hours of monitoring (mean watch length: 113.6 ± 17.3 min, $n = 13$), 67 female visits were observed, but no male was ever witnessed to visit, provision or brood the chicks. The average visit rate by females was 3.04 ± 0.80 visits/hour (range: 1.20-4.94; $n = 4$ females). Females spent on average 7.7 ± 1.3 minutes (range: 0.1-46.0 min; $n = 58$) at the nest during each visit, and 11.8 ± 1.3 minutes (range: 1.5-59.9 min; $n = 55$) away from the nest between visits. It was not possible to confirm whether the chicks were provisioned on every visit. Time spent at the nest during nocturnal focal watches was negatively correlated with minimum ambient temperature (Spearman rank correlation: $r_s = -0.81$, $n = 13$, $P < 0.005$). In 100% (10 of 10) of daytime checks during the chick period, the

female was found to be present at the nest site, either brooding or immediately adjacent to the chicks.

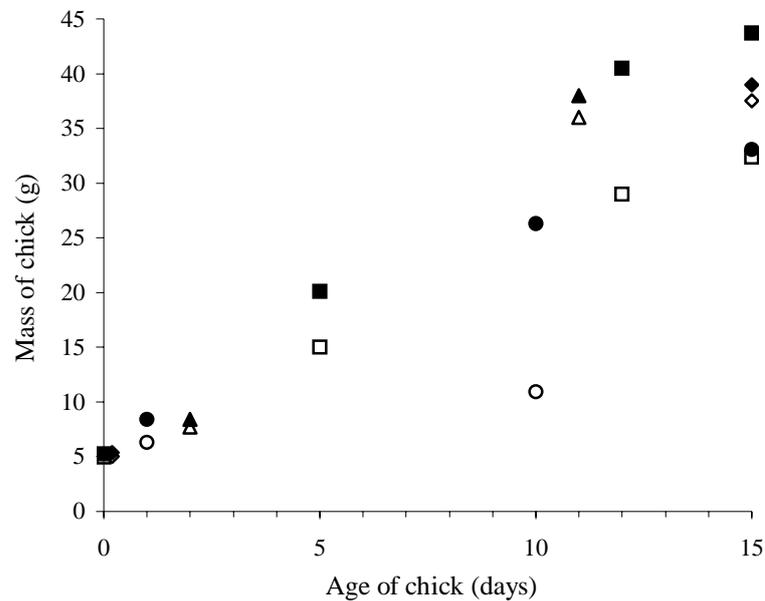


Figure 3.6 Growth rate of eight nightjar chicks between hatching and 15 days of age. Each brood represented by different shape; open and closed symbols represent two chicks within same brood. Four chicks weighed on day 0 had masses of *c.* 5 g (square and diamond symbols).

Females displayed a range of anti-predator behaviours whilst incubating or brooding. When initially approached, the female relied on her cryptic plumage, crouching motionless with her eyes closed to slits. If the intruder approached to within 0.5-2.0 m, she would shuffle forward into the adjacent clearing in preparation for take-off. On one occasion, a female incubating a single, recently-laid egg was observed to perform a presumed threat display: drooping the wings slightly, puffing up the body feathers, raising and slightly splaying the tail, whilst rocking the body and tail from side-to-side. When eventually flushed, females typically performed an injury-feigning distraction display, flying 5-10 m away from the nest with a low, laboured flight, before landing clumsily in the vegetation. If approached again, the female would fly off normally, though on most occasions she was subsequently found to have remained in the vicinity of the nest site.

By the time they were one week old, chicks were already highly mobile and had begun to lose their natal down and attain the plumage pattern of adult birds. After about ten days, the developing flight feathers began to project from their feather sheaths. Unfortunately, it was not possible to confirm the exact age at which chicks fledged from any of the nests monitored. However, extrapolation of observed growth rates suggested that chicks may attain mean adult mass (*c.* 50 g) at *c.* 19 days old. The sole surviving chick of one clutch present on day 18 could not be relocated on day 20.

Due to the uncertainty over the final fate of most broods, it was not possible to calculate estimates of fledging success or overall nesting success. Predation of both eggs and chicks was noted during this study, but on neither occasion was the identity of the predator confirmed (Table 3.7). One female moved her chicks to a new clearing, *c.* 10 m from the original nest site, when they were about ten days old. Assumptions about the fate of other broods, based solely on the disappearance of chicks from the original nest site, therefore seem inappropriate. None of the chicks captured and ringed at the nest site was recaptured following fledging during the current study. However, one chick ringed in October 2000 was recaptured as a yearling male in December of the following year (J. Mazar Barnett *in litt.* 2002).

Chick paternity

Blood samples were obtained from four breeding females and eight of their chicks during the 1999 and 2000 breeding seasons (Table 3.10). Samples were also collected from 23 of 26 males captured between 1998 and 2001, including all those with display territories in the vicinity of nests found during 1999 and 2000. The seven primer pairs produced 121 polymorphic AFLP fragments, as assessed by band absence in at least one individual. A single set of probable parents was identified for all eight chicks using paternity exclusion. The expected female was identified as mother for all eight chicks. In five cases, the most probable parental combination identified from AFLP profiles explained all of the chick's bands; for three chicks there was a discrepancy of one or two bands. The next most probable adult pair showed a discrepancy of five bands with the chick profile in the latter cases. The same male was proposed to have sired both offspring in each of the three broods where two chicks were sampled. The postulated father for each brood had a display territory within 450 m of the nest site. However, in two cases (NT067A in 1999 and NT066D in 2000; Figure 3.7), he was not actually the nearest territory-holding male. In 1999, one male (M001) was shown to have sired the chicks of at least two different females.

Table 3.10 Parentage of nightjar chicks from 1999 and 2000 breeding seasons as revealed by AFLP analysis.

Chick(s)	Season	Nest	Mother	Father
J017	1999	NT067A	F067	M001
J018	1999	NT063B	F063	M001
J022/J023	2000	NT010A	F010	M020
J029/J030	2000	NT010B	F010	M020
J027/J028	2000	NT066D	F066	M057

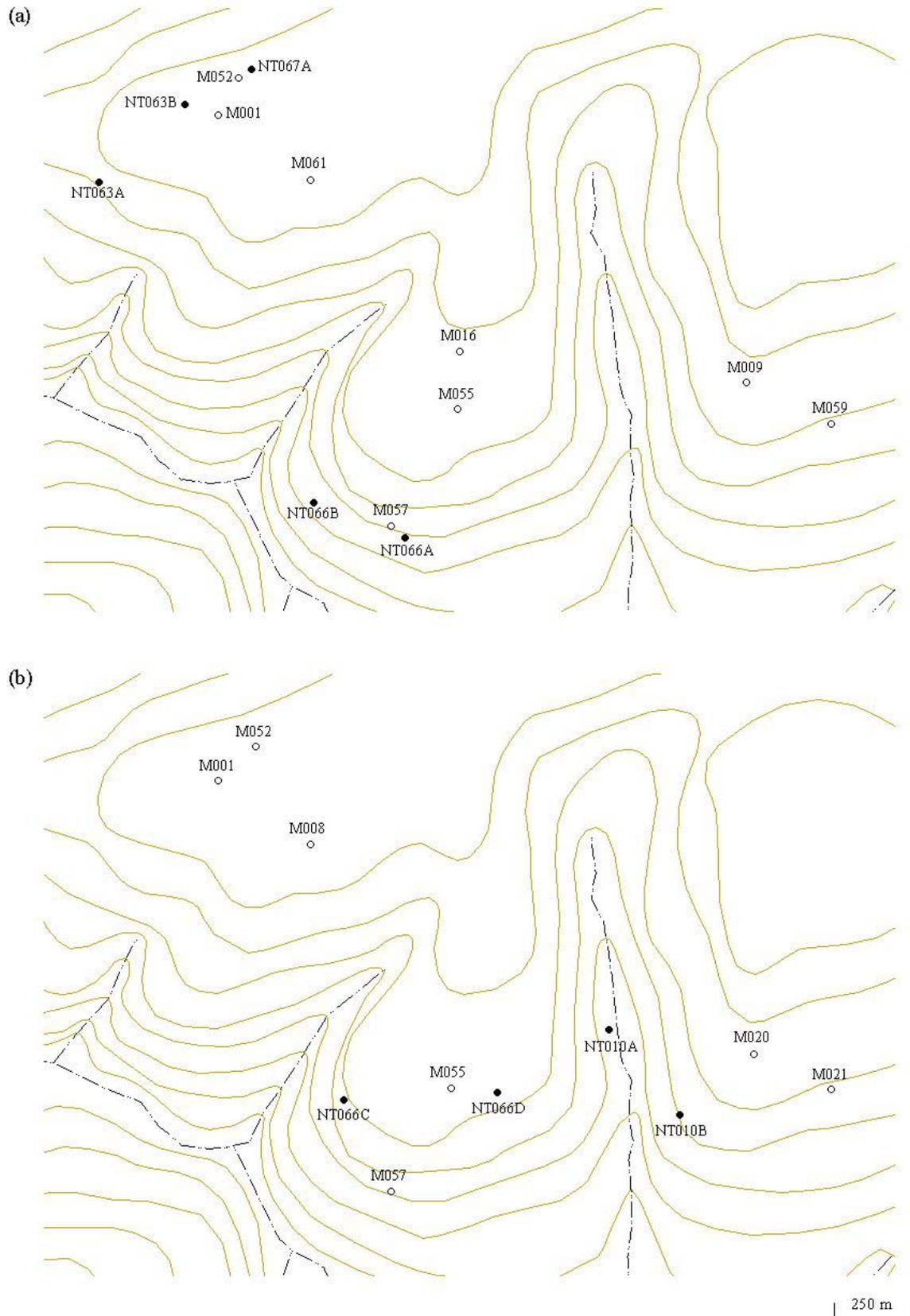


Figure 3.7 Distribution of nest sites in relation to male display arenas during: a) 1999 and b) 2000 breeding seasons. Nest sites displayed as filled circles; multiple nesting attempts distinguished by 'A', 'B', etc. Display arenas displayed as open circles; labels refer to the territory-holding male.

DISCUSSION

During the breeding season, male White-winged Nightjars defended small display territories on the upper slopes of low ridgelines in the southern sector of Aguará Ñu. Patterns of territory usage and ownership observed during the current study supported the suggestion of Clay *et al.* (2000) that display territories are traditional. Quantitative analysis of their spatial distribution confirmed that display arenas were significantly aggregated within the survey area, with neighbouring males separated on average by distances of *c.* 250 m. Although relatively few nesting attempts were documented during the current study, nest sites were found to be on average 227 m from the nearest display arena, with no compelling evidence to suggest that they fell within the boundaries of male display territories (see also Chapter 4). Moreover, chick paternity analyses showed that the nearest territory-holding male was not always the father of a brood. Males apparently played no part in the parental care of eggs or chicks, and females were only rarely observed in the vicinity of display territories, with anecdotal evidence suggesting that they mainly visited around full moon when potentially seeking copulations.

With a few notable exceptions (e.g. Ingels *et al.* 1984, Roth 1985, Vilella 1995, Cleere & Ingels 2002), detailed studies of the nesting biology of Neotropical nightjars are surprisingly sparse. Nevertheless, the information presented herein for the White-winged Nightjar broadly coincides with that available in the literature for other *Caprimulgus* species (summarised in Cleere 1998, Cleere 1999, Holyoak 2001). Like most birds, nightjars breed when food is most abundant for raising young (Lack 1968, Holyoak 2001), and the study species appears to be no exception. As with most other grassland birds at the study site (pers. obs.), nesting activity occurred during the austral spring and summer, and hence coincided with the onset of the heavier summer rains (Figure 1.3). Mass hatches of winged termites and ants were a regular occurrence at the study site during the summer months (see also Lubin 1983, Pinheiro *et al.* 2002), and may have represented a sporadically abundant food source for female nightjars provisioning young (see Jackson 2000a,b).

At a finer scale, the timing of White-winged Nightjar nesting attempts within the breeding season showed remarkable synchrony with the full moon. A relationship between nest initiation date and moon phase has been demonstrated for a number of nightjar species (e.g. Jackson 1985, Mills 1986, Vilella 1995, Perrins & Crick 1996; but note Brigham & Barclay 1992), and authors typically emphasise the advantages of high levels of moonlight for foraging during the first two weeks of the nestling period. The modal incubation period of 19 days observed for White-winged Nightjars did result in chicks hatching between the new moon and first quarter, and hence during a period of increasing moonlight. However, with male investment in the next generation apparently limited to genes, it might be argued that females utilise periods of high moonlight to assess the quality of

potential fathers before securing copulations. Of course, these two suggestions may not necessarily be mutually exclusive.

Male nightjars displayed for a relatively prolonged period between late August and early January, coinciding with the vocal activity of most other sympatric Caprimulgiforms. Although there was considerable variation in display rate within this period, this was apparently due more to environmental conditions than to consistent individual differences in display effort. High levels of activity were observed when males first arrived at display arenas at dusk, but this was often relatively short-lived and may have been analogous to the dawn peak of song activity noted for many diurnal birds. Various reasons have been proposed to explain the latter phenomenon, some of which may also be applicable to a dusk peak for nocturnal species, e.g. signalling survival to rival males (Kacelnik & Krebs 1982) or synchronising with female behavioural patterns (Mace 1987). Alternatively, the peak in nightjar activity may be related to the spectral properties of ambient light at dusk – a visual equivalent of the “good acoustic conditions” hypothesis (Henwood & Fabrick 1979) – as demonstrated by Andersson *et al.* (1998) for the crepuscular and lek-mating Ghost Swift Moth *Hepialus humuli*. Unfortunately, it was not possible to measure absolute levels of ambient light during the current study, but the moonlight estimate used as a surrogate did show some predictive power for male display rate under conditions of true night. Given that increases in vocal activity have been noted for various nightjars under conditions of increased moonlight (e.g. Brauner 1952, Cooper 1981, Mills 1986), it is not surprising that a similar relationship should exist for a species with such a strong visual component to its display.

The results of the current study support previous suggestions that the “tk” and “grrrrrt” components of male display noises are both mechanical, rather than vocal, in origin (Clay *et al.* 2000). Careful observation showed that the “tk” noise was not produced by clapping of the wings below the body, as postulated by Clay *et al.* (2000), but probably by contact with the display mound. On the other hand, there was little doubt that the “grrrrrt” noise was produced by the wings during the male’s near-vertical ascent from the display mound. The production of mechanical sounds is a relatively rare phenomenon in birds (Bostwick 2000), but similar mechanical wing noises have been documented for other nightjars, including the closely related Sickle-winged Nightjar *Eleothreptus anomalus* (Straneck & Viñas 1994). Prum (1998) noted that the evolution of mechanical sound production in birds is often associated with acrobatic, polygynous courtship displays, and this would appear to hold true in the case of the White-winged Nightjar.

The inter-individual variation in display noise noted during this study raised the question of whether certain variables – such as the length of the “grrrrrt” – might represent reliable signals of male quality. Unfortunately, the data collected were too sparse to investigate this possibility in any

detail, but the observation that “grrrrt” length increased between seasons for four males recorded in both 1999 and 2000 (significantly so for three: $P < 0.05$; Mann-Whitney U -tests) suggests that this measure may vary with age or experience. There was, however, no significant correlation between “grrrrt” length and the estimate of wing curvature used in Chapter 2 (Spearman rank correlation: $r_s = 0.55$, $n = 8$, $P > 0.05$).

Overall, the evidence from this study indicated that the population of White-winged Nightjars at Aguará Ñu exhibits a polygynous mating system. Male emancipation from parental care is an important prerequisite for any form of polygyny (Höglund & Alatalo 1995), but is unexpected in altricial bird species if fledging success is limited by the amount of food brought to the nestlings (Oring 1982). Snow & Snow (1979) proposed three ecological attributes that favour the evolution of male emancipation in altricial bird species: frugivory; the ability to regurgitate food; and roofed nests (in rainy season breeders). Nightjars are well known to regurgitate food for their chicks (e.g. Cramp 1985, Sick 1993, Cleere 1999), and this ability probably facilitates maximal provisioning efficiency per trip away from the nest. Moreover, for species of tropical savanna habitats, the seasonal abundance of certain insect prey during the summer rains (Pinheiro *et al.* 2002) might be analogous to the periodic super-abundance of food associated with frugivory.

Although the population of White-winged Nightjars at Aguará Ñu appeared to fulfil all four of the criteria stipulated by Bradbury (1981) for lek-mating species (see Introduction), the exact nature of the mating system remains uncertain. The inter-male distances observed in the current study far exceeded those typical of so-called ‘classical’ lekking species, and approached the upper limit of those of ‘exploded’ or ‘dispersed’ avian leks (e.g. Théry 1992, Tello 2001, but note Alvarez Alonso 2000). Moreover, the question of whether males were aggregated for social reasons, or solely as a result of the patchy availability of suitable display habitat, remains unanswered. If the latter is true, and males were spaced regularly *within* the available habitat (e.g. Pruett-Jones & Pruett-Jones 1982), the study species might best be described as exhibiting a ‘landmark’ mating system. This term has traditionally been reserved for insect species in which males aggregate on hilltops or in forest clearings (e.g. Alcock 1981), but is applicable to any taxon using a specialised habitat to provide encounter sites for mating (Höglund & Alatalo 1995). Although the evolutionary causes of aggregation in landmark species differ from those for classical lekking species, females of the former do also visit male aggregations primarily for the purpose of mating, and hence still fit the broad definition of lekking proposed by Höglund & Alatalo (1995).

CONCLUSIONS

This chapter represents the first comprehensive study of the breeding biology of the White-winged Nightjar. The practical implications of the findings for the conservation of the study species are

highlighted and discussed further in Chapter 6. Nonetheless, the behavioural evidence outlined above confirms that the study population of White-winged Nightjars does exhibit a polygynous mating system, and also meets the four lekking criteria of Bradbury (1981). The reasons why polygyny and male emancipation have evolved in the White-winged Nightjar but in few other nightjar species (see Chapter 5) remain uncertain, and this topic is revisited in Chapter 6. However, the evolution of mating systems is greatly influenced by the spatial distribution of mates and resources, and it is the spatial aspects of nightjar ranging behaviour and resource use that are the focus of Chapter 4.



(a)



(b)



(c)



Plate 3.1 Male display arenas and behaviour: (a) male display arena in open campo cerrado habitat; (b) close-up of typical arena showing 'towers'; (c) and (d) male during display activity, showing conspicuous white plumage of wings and tail.



(a)



(b)



(c)



(d)

Plate 3.2 Nest site, eggs and chicks: (a) female nightjar roosting behind eggs at nest clearing; (b) clutch of two eggs showing subtle differences in markings between eggs; (c) and (d) two chicks of F063, at 3 and 14 days old: note underdeveloped 'runt' in latter.

CHAPTER 4

RANGING BEHAVIOUR AND HABITAT USE OF WHITE-WINGED NIGHTJARS IN PARAGUAY

SUMMARY

This chapter presents the results of the first quantitative study of the ranging behaviour and habitat preferences of the White-winged Nightjar. Nine radio-tagged nightjars were monitored for periods of up to ten months between August 2000 and June 2001. Of these, two females and three males were followed for eight months or more, spanning both the breeding (August to December) and non-breeding (January to June) seasons. Maximal home-range estimates (from 100% minimum convex polygons) for these individuals averaged 28.0 ± 4.2 (range: 19.0-41.4) hectares. The use of non-MCP methods of range analysis helped to highlight the patchy usage of home ranges by nightjars. For each of the five individuals, 90% of radio-tracking locations were encompassed within three to six 'core areas' (identified by cluster analysis) occupying just $8.8 \pm 1.2\%$ of the overall range area. Despite some overlap in MCP ranges, the core areas of neighbouring nightjars were virtually non-overlapping. No evidence was obtained to suggest that the species was migratory. The size and location of the home ranges of two female nightjars changed little between the breeding and non-breeding season. Male nightjars, however, showed somewhat restricted ranging behaviour during the breeding season: 97% of nocturnal fixes from seven males fell within 150 m of their display arenas. Patterns of habitat use differed from random at both of the spatial scales inspected. Nightjar home ranges contained no forested or older campo cerrado habitats, but a higher proportion of young campo cerrado than the study area as a whole. At a finer scale, nightjars preferred younger and avoided older campo cerrado habitats when selecting foraging sites within their home ranges. Wet grassland was used roughly in proportion to its availability. Although estimates of moth abundance were influenced primarily by climatic conditions, some evidence was obtained to suggest that younger habitats supported more insect prey than older habitats. Three nightjars avoided a burn parcel that partially overlapped with their ranges for at least eight weeks following the experimental burn, suggesting that there was some delay before birds 'recolonised' areas after a fire. When selecting daytime roosts within their home ranges, nightjars preferentially avoided the youngest and oldest habitats, reflecting their apparent need for sites that provided a balance between vegetation cover and access. Observations of nightjars inactive at roost sites on nights in May and June suggested that individuals may occasionally enter torpor on cold nights, but this was never confirmed physiologically.

INTRODUCTION

Habitat loss or degradation is a major cause of endangerment for 85% of the world's threatened birds (BirdLife International 2000). For many species, however, conservation efforts are hampered by an acute lack of information on their habitat requirements. Understanding a species' requirements for key activities such as foraging, nesting and roosting is essential for the success of any management measures (Caughley 1994, Sutherland 1998). Increasingly, radio-telemetry is the preferred technique for studying a species' ranging behaviour and habitat usage (e.g. Bramley & Veltman 2000, Ratcliffe & Crowe 2001, Wiklander *et al.* 2001), and although radio-telemetry methods are not entirely free from bias (see e.g. Rettie & McLoughlin 1999), their usage can mitigate several problems associated with visual methods, such as differential detectability of individuals between habitats. The advantages of radio-tracking are particularly pertinent in the case of nocturnal species, many of which would be almost impossible to monitor using visual methods alone. It is therefore not surprising that radio-telemetry has played a central role in several previous studies of nightjar ranging behaviour and habitat use (e.g. Alexander & Cresswell 1990, Wang & Brigham 1997, Sierro *et al.* 2001).

The White-winged Nightjar *Caprimulgus candicans* is endemic to the Cerrado region of central South America (Silva 1995), where it is known from a small number of grassland sites in Brazil, Bolivia and Paraguay (Chapter 1). Although considered threatened by the wholesale destruction and degradation of its cerrado habitats (BirdLife International 2000), its habitat requirements at a finer scale remain poorly understood. Observations have indicated that it favours open grassland habitats (Collar *et al.* 1992, Lowen *et al.* 1996b), and certain authors have suggested that it may prefer recently burnt areas (Lowen *et al.* 1997, Rodrigues *et al.* 1999). Preliminary radio-tracking work conducted in 1997 at the site of the current study provided the first data on the species' activity patterns and foraging behaviour, and on the vegetation characteristics of its daytime roost sites (Capper *et al.* 2000). A sighting of an adult male in burnt campo cerrado vegetation, just six days after an extensive grassland fire, also provided some support for the species' postulated preference for recently burnt habitats.

Wildfires are a natural factor shaping tropical savannas around the world (Andersen *et al.* 1998), and periodic burns have occurred in the cerrados of central South America for at least 34,000 years (Silveira *et al.* 1999). Lightning is the main cause of natural fires in most ecosystems, but nowadays most fires in the Cerrado region are the result of human agricultural activity, started to promote fresh regrowth for cattle pasture or to clear land for crop planting (Coutinho 1990, Mistry 1998). These anthropogenic burns occur almost exclusively during the local dry season (Cavalcanti 1988), and often spread uncontrolled into conservation zones, where they can burn extensive areas before finally subsiding (Redford 1985, Silveira *et al.* 1999). Grassland fires are a

regular occurrence at Aguará Ñu, the site of the current study, occurring mainly during August and September, prior to the onset of the summer rains (Capper *et al.* 2000; Chapter 1). Although the cerrado is a fire-adapted environment (Pivello & Norton 1996), the timing, frequency and extent of modern burns may pose a serious risk to the ecological equilibrium of the system (Coutinho 1990).

In this chapter, I provide the first quantitative description of the ranging behaviour and habitat use of the White-winged Nightjar, using data collected during a three-year study in Paraguay. Radio-telemetry data are used to estimate the size, configuration and overlap of nightjar home ranges, during the breeding and non-breeding seasons, and patterns of habitat selection are inspected at two spatial scales. First, the habitat composition of nightjar home ranges is compared with that of the study area. Second, habitat selection is investigated at a finer scale within home ranges. Since nightjars might require different habitats for foraging and roosting, these two key activities are considered separately. Patterns of habitat usage can be interpreted only in the context of the habitats available to individuals, so data are also presented on the response of three radio-tagged nightjars to an experimental burn conducted in part of their home ranges. Descriptive information is also provided on the feeding ecology and roosting behaviour of nightjars, to help explain the patterns of habitat selection observed.

METHODS

Fieldwork was conducted between 1998 and 2001 at Aguará Ñu, an area of natural grassland and cerrado habitats in eastern Paraguay (Chapter 1). Some preliminary radio-tracking work was carried out during 1998 and 1999, but most data were collected between August 2000 and June 2001 (the '2000/1 season'). Adult nightjars were captured, sexed and ringed as detailed in Chapter 2, and fitted with a TW-4 radio-transmitter with a 20-cm flexible NiTi wire antenna (Biotrack Ltd., Wareham, Dorset). Depending on the type of button cell fitted, transmitter weights varied between 1.3 and 2.5 g, but never exceeded 5% of body weight, as recommended for birds of less than 70 g (Aldridge & Brigham 1988). Following the premature loss of several tail-mounted transmitters in 1998, all tags were back-mounted during 1999 and 2000/1, using a 'back-pack' harness design with two elastic wing loops. The battery life of tail-mounted transmitters was approximately 9 to 11 weeks, whereas the heavier back-mounted transmitters lasted between 12 and 25 weeks.

Tagged nightjars were located using a Mariner M57 portable receiver (Mariner Radar Ltd., Lowestoft, Suffolk) and a hand-held 3-element Yagi aerial (Biotrack Ltd.). Several factors influenced the distance from which transmitters could be detected, most notably local topography, the activity of the focal bird, and the position of the tag antenna in relation to the aerial. While it was sometimes possible to obtain a signal from over 1 km away, especially from elevated

locations, generally the signal range coincided with the “200-600 m” cited on the Biotrack website (www.biotrack.co.uk). The open habitat and relatively long distances from which nightjar eye-shine was visible meant that a ‘homing’ technique (White & Garrott 1990) was adopted in the current study, following transmitter signals until tagged birds could be seen. Although time-consuming, this method provided more reliable locational data than triangulation. It also allowed the collection of behavioural data, as well as visual confirmation of the habitat and perch used by a bird. All radio-tracking locations were recorded using a Magellan 2000 XL GPS receiver, which provided positional data to a precision of one metre. In practice, fixes were probably only accurate to tens of metres, although accuracy improved to *c.* 5-10 m following the deactivation of ‘selective availability’ in May 2000 (www.igeb.gov). Where sites were used repeatedly (e.g. nests, roosts, male display mounds), the arithmetic mean of all fixes obtained for each site was used in subsequent analyses.

During 1998 and 1999, radio-telemetry was utilised primarily on an *ad hoc* basis to locate nests and daytime roosts. However, to determine the most appropriate monitoring regime for the main study in 2000/1, a trial period of continuous radio-tracking was conducted during July-August 1999. The patterns of movement observed during this trial were ill suited to continuous monitoring (see Results), and so a discontinuous radio-tracking regime was selected for the main study. To ensure that the data provided a representative sample of each individual’s ranging behaviour, a sampling protocol was followed whereby locations were obtained at all stages of the night and throughout the relevant study period.

Many statistical methods of home-range analysis assume the independence of successive locations, so it was important to ensure that radio-tracking fixes were not temporally auto-correlated (Harris *et al.* 1990, White & Garrott 1990). The method outlined by Swihart & Slade (1985) was used to investigate the extent of temporal auto-correlation in the 1999 trial data, and hence identify an appropriate sampling interval for the main study. All locations collected during 2000/1 were separated by this minimum sampling interval: in practice, this meant that only one location per night was used in subsequent analyses. The only exceptions were two nesting females, for which two locations were collected on a small number of nights, to obtain a sufficient number of foraging fixes. Although, strictly, these locations were temporally auto-correlated, they were considered to be ‘biologically independent’ (*sensu* Lair 1987), as the female had returned to her nest between fixes, and hence made two independent foraging decisions.

Home ranges

A wide variety of analytical techniques exists for estimating home-range size and determining patterns of home-range utilisation (reviews in Worton 1987, Harris *et al.* 1990, White & Garrott 1990). Each method has its advantages and limitations, and three different techniques are provided for comparison in this study: minimum convex polygons, kernel analysis and cluster analysis. All analyses were carried out using the Ranges V program (Kenward & Hodder 1996).

Minimum convex polygons (MCPs) are one of the oldest and simplest methods of estimating home ranges, and traditionally the most commonly used (Mohr 1947, Harris *et al.* 1990). Their boundaries are determined by peripheral fixes, and so they often include large areas never visited (White & Garrott 1990), but 100% MCPs provide satisfactory estimates of maximal home ranges, and represent the most useful method for comparison with other studies (Harris *et al.* 1990). As they are strongly influenced by the number of locations obtained, it is important to check that sample sizes are sufficient to ensure stable estimates of home-range area. Plots of cumulative home-range size *versus* the number of fixes collected were inspected to confirm that area estimates reached clear asymptotes for every range (see Results). Locations were excluded in a random order, as recommended by Harris *et al.* (1990) for discontinuous data, and any changes in range area were recorded. As an estimate of the 'normal' home range used by nightjars, 95% peeled polygons (95% MCPs) are also presented, obtained by excluding the 5% of outlying fixes furthest from the range centre. In this study, the harmonic mean fix was used to define the range centre, since it provides a more robust estimator than the simple arithmetic mean (Dixon & Chapman 1980).

Kernel analysis is a non-parametric, probabilistic method of estimating the utilisation distribution, capable of representing home ranges of any shape (Worton 1989). The accuracy of kernel estimates is dependent on both the smoothing factor (h) and kernel method selected. In the current study, the fixed kernel method was used, since the adaptive kernel technique is prone to unacceptable expansion of the outermost contours (Kenward & Hodder 1996). The least squares cross validation method of smoothing factor selection was also attempted, as recommended by Seaman & Powell (1996), but the Ranges V program failed to identify optimal values of h for any of the home ranges tested. The method outlined by Wray *et al.* (1992) was instead used to select the most appropriate value of h . In all cases, the 95% kernel isopleth was used as the estimate of home-range size.

Cluster analysis is particularly useful for eliminating outlying fixes and highlighting patchiness in range usage (Kenward & Hodder 1996). It is often used to define core areas by identifying zones of high usage (Robertson *et al.* 1998), and describes multinuclear ranges more effectively than polygon-peeling methods. The technique works by identifying groups of three or more closely aggregated fixes, which are then expanded and/or merged according to rules based on nearest-

neighbour distances. Once the specified percentage of fixes has been incorporated, clusters are delimited using convex polygons (Kenward 1987). The percentage of locations that best defined range cores – 90% in this study – was identified from the point of inflection on a multi-range plot of mean areas versus proportion of fixes (see Harris *et al.* 1990, Kenward & Hodder 1996).

Habitat use

To characterise habitat selection by nightjars, patterns of habitat use were inspected at two spatial scales and tested for departure from random (Jones 2001). First, the habitat composition of nightjar home ranges was compared with that of the whole study area (see below), to investigate any broad patterns of ‘second-order selection’ (*sensu* Johnson 1980). Simple comparisons of used *versus* unused habitats can, however, be misleading, since they make assumptions regarding habitat availability, without taking into account extrinsic factors such as territoriality. Hence, patterns of fine-scale habitat use (i.e. used *versus* available habitats within home ranges) were also inspected to characterise any ‘third-order selection’ (*sensu* Johnson 1980). This was done separately for nocturnal (‘foraging’) and diurnal (‘roost’) fixes, in case nightjars showed different habitat preferences during these two key activities.

For the purposes of habitat analyses, the ‘study area’ was delimited by a convex polygon, encompassing the home ranges of all relevant nightjars, but with no boundary closer than 75 m to the edge or vertices of any home range (see Results). The habitats present within the study area were allocated to one of three types: (i) *campo cerrado*, cerrado grasslands on dry soils with scattered shrubs and trees (principally ‘yata’i palms *Butia paraguayensis*); (ii) *wet grassland*, permanently or seasonally saturated grasslands, lacking shrubs or trees; (iii) *forest*, isolated forest stands and gallery forest along the principal water courses. A geo-referenced black-and-white aerial photo, imported as a layer into a geographical information system (GIS) in ArcView 3.2 (ESRI 1999), clearly showed the boundaries between the three habitat types, allowing them to be mapped ‘on-screen’. Since grassland fires are a regular occurrence at the study site, the two non-forest habitats were subdivided into three age classes according to when they were last burnt. GPS locations taken from the boundaries of burns between 1998 and 2000 were used to add this age data to the habitat map. Details of these age classes are provided in Table 4.1. The resulting number of habitat categories was seven: one forest and six non-forest. Due to the limited distribution of the ‘wet grassland (00)’ and ‘wet grassland (97)’ categories, it was necessary to combine all wet grassland age classes as a single category for the purposes of habitat-use analyses (but *cf.* ‘Feeding ecology’). The accuracy of the final habitat map was assessed by overlaying all radio-tracking fixes for which habitat details had been noted in the field: all locations ($n = 215$) fell within the correct category on the map.

Table 4.1 Age classes and burn dates for habitats present within the *c.* 300 ha study area.

Age class	Date of burn(s)	Details
2000	7 October 2000	<i>c.</i> 15 ha burnt midway through breeding season
1999	2 August 1999 ^a	Extensive burn, affecting much of Aguará Ñu
	15 May 1999 ^a	Burn of <i>c.</i> 20 ha
1997	17 August 1997	Extensive burn in southern zone of Aguará Ñu

^a Burns combined in single '1999' age class for habitat-use analyses (*cf.* 'Feeding ecology').

A wide range of analytical techniques is available for studying habitat selection (reviews in Alldredge & Ratti 1986, Thomas & Taylor 1990, White & Garrott 1990). In recent years, compositional analysis (Aebischer *et al.* 1993) has become the technique favoured by many authors, but the small number of individuals in the current study precluded its use. Instead, a technique based upon the χ^2 analysis proposed by Neu *et al.* (1974) was used to investigate whether habitat use differed from that expected on the basis of habitat availability. This method retains the assumptions of the standard χ^2 test, and it proved necessary to pool fixes across individuals to ensure that all expected values met the necessary requirements. As this can result in the loss of inter-individual variation (White & Garrott 1990), plots illustrating individual selection variability are also provided, as recommended by Thomas & Taylor (1990). For three individuals, it was only possible to use data collected following the October 2000 burn, as the habitat composition of their home ranges effectively changed midway through the breeding season. Where usage was shown to differ significantly from random, Bonferroni confidence intervals were calculated to confirm which habitats were significantly preferred or avoided (see 'Statistical analysis').

To investigate the response of nightjars to a limited fire within their home ranges, an experimental burn was planned and carried out with the approval and logistical assistance of the Fundación Moisés Bertoni. The location of the *c.* 9-hectare (300 x 300 m) burn parcel was selected to overlap with the home ranges (mean overlap: $28.1 \pm 2.3\%$ of 100% MCP) of three radio-tagged nightjars. Unfortunately, for logistical reasons, it was not possible to carry out the controlled burn until July 2001, after the formal conclusion of fieldwork. However, occasional radio-telemetry monitoring work was conducted by field assistants over the course of eight weeks immediately following the burn. Since the purpose of the experimental burn was explicitly to investigate post-burn habitat selection by nightjars, habitats were simply categorised as 'burnt' or 'non-burnt' and post-burn patterns of usage were analysed using the two-cell *G*-test for goodness of fit.

Feeding ecology

Ad hoc monitoring of radio-tagged nightjars prior to the current study suggested that they hawked for insects during uninterrupted flight for a brief period at dusk, before reverting to a 'sallying' or

‘sit-and-wait’ strategy for the rest of the night (Capper *et al.* 2000). To obtain further information on feeding behaviour, informal foraging watches were conducted during the trial period of continuous radio-tracking in July and August 1999. During these watches, focal birds were monitored visually for variable periods of time, and the number and time of all sallies were recorded. A torch set on diffuse beam was used to obtain eye-shine from the focal bird without unduly disturbing it. However, it was not possible to identify target prey items, or indeed confirm whether sallies were successful, in the vast majority of instances.

To investigate variation in prey abundance between habitats of different type and age, moth counts were conducted on five nights during September–November 1999, using a method based upon the “horizontal beam method” of Bowden & Green (1994). Six survey stations were established within a zone of *c.* 30 ha where the two dominant habitat types (campo cerrado and wet grassland) and three age classes (Aug-97, May-99 and Aug-99) intersected. The relative proximity of the six stations meant that it was possible to visit them all within a period of 60 minutes, thus limiting any variation in moth abundance resulting solely from changes in environmental conditions. A different visit order was used on each occasion. At each station, a 4-cell Maglite torch was held at chest-height with the beam horizontal, and the number of moths crossing the beam between the observer and a marker 40 metres away was recorded during ten 10-second count periods. The torch was turned off for 20 seconds between counts to avoid actively attracting moths into the survey area. Counts were made only on dry nights with little or no wind (Beaufort number ≤ 4). Two shifts of counts were conducted on each night of surveys: one approximately an hour after sunset, the second around midnight.

Roosting behaviour

Nightjar roost sites were identified by locating radio-tagged individuals during daylight hours. The cryptic nature of roost sites and unobtrusive behaviour of roosting nightjars meant that birds were occasionally flushed up from roosts before their exact location had been confirmed visually. However, with experience it became possible to identify the precise sites used without disturbing roosting birds. The location of each roost was recorded using a GPS receiver, noting the habitat type and age class, and the orientation of the roosting bird was allocated to one of four quadrants (north-east, south-east, south-west and north-west).

To investigate the fine-scale habitat preferences of roosting nightjars, the characteristics of twelve roost sites used between February and May 2001 were measured, and compared with those of an equal number of random sites. A 1-m² quadrat, divided into four equal 0.5 x 0.5 m sub-quadrats, was centred on each roost site, and eleven measures of vegetation composition and structure were taken (see Table 4.8). Estimates were made of the percentage cover of the three main vegetation

classes (grasses, herbs and woody vegetation) and of bare soil. The maximum height of each vegetation class was measured, to the nearest 5 cm, in each of the four sub-quadrats, and a mean calculated. The number of adult yata'i palms and woody saplings (over 1 m tall) within a 5-m radius of the roost site was also recorded. An estimate was made of local yata'i density using the *T*-square method, a plotless sampling technique that uses pairs of distances (from a random point to the nearest palm, then from the latter to its nearest neighbour) to provide an estimation of individual density (Sutherland 1996). In the current study, nine such pairs of distances were measured for each roost site: from the roost itself, and also 20 m out on eight points of the compass. Finally, an estimate was made of the overhead cover, by positioning a bright red nightjar-sized object at the exact site of the roosting bird, and estimating the proportion obscured by vegetation when viewed from above (see Wang & Brigham 1997). Roosts were surveyed within five days of last being used, with the 'paired' random site measured on the same day, to control for any potential changes in vegetation structure during the sampling period. The location of random sites was determined using random tables of distances (< 150 m) and compass bearings. All random sites were selected to fall within the same habitat type and age class as their paired roost.

Statistical analysis

All continuous data were tested for normality and homoscedasticity prior to analysis with standard parametric and non-parametric univariate tests. In the case of the vegetation characteristics of roost sites, where the dependent variable could be allocated to one of two discrete categories (i.e. roost site or random site), binary logistic regression was used to identify which combination of variables best distinguished between the categories (see Chapter 3). Categorical data were analysed using the *G*-test for goodness of fit. Statistical significance was set at $P < 0.05$, unless otherwise specified. Means are given \pm one standard error.

Patterns of habitat usage were inspected using a technique based upon χ^2 analysis, but adapted for the *G*-test for goodness of fit. Where this revealed non-random habitat use, the Bonferroni confidence interval technique (Neu *et al.* 1974, Byers *et al.* 1984) was used to confirm which habitats were significantly avoided or preferred. Sets of simultaneous confidence intervals were calculated for the observed proportions of utilisation (p_i) of habitat categories, adjusting the initial α -value of 0.05 for the number of habitats being tested. Where the expected proportion of utilisation (P_{io}) of a habitat fell outside these confidence intervals, the expected and observed usage differed significantly, and the habitat was preferred or avoided.

RESULTS

Four nightjars were monitored continuously for periods of 165 to 320 minutes on six nights during July and August 1999. This trial study showed that individuals spent spells of up to 233 minutes at perches (mean: 52 ± 14 mins, $n = 18$ occasions on which both arrival and departure times known), punctuated by rapid movements of 206 ± 55 metres. Analyses showed that radio-tracking locations were temporally auto-correlated at sampling intervals of up to 150 minutes (the maximum tested). Consequently, a discontinuous radio-tracking regime was adjudged most appropriate for the 2000/1 study, collecting just one location per individual on any particular night (but see also Methods).

During the 2000/1 season, nine nightjars were radio-tracked for periods ranging between two and ten months. Five individuals (two females and three males) were monitored for eight months or more, from August-October at the start of the 2000 breeding season until the end of the following non-breeding season in June 2001 (Table 4.2). An average of 53.6 (range: 43-63) radio-tracking locations was obtained for these five individuals, distributed in an approximately uniform fashion across the tracking period. Due to logistical problems, no radio-tracking work was conducted in January 2001, but fixes were collected every 4.8 ± 0.2 days on average during the rest of the study period. The remaining four individuals (all males) were radio-tracked only during the breeding season (August to December 2000). One male (M061) disappeared after just ten weeks of monitoring and was never relocated.

Table 4.2 Summary of radio-tracking effort and estimates of home-range size for two female and three male nightjars monitored between August 2000 and June 2001.

Individual	Tracking period	No. of fixes	Estimates of home-range size (ha) ^a			
			100% MCP	95% MCP	95% KER	90% CLU
F010	Oct-00 - Jun-01	43	34.24	25.12	31.57	3.00
F066	Aug-00 - Jun-01	63	22.83	22.21	20.81	2.01
M052	Aug-00 - Jun-01	53	41.40	25.85	36.86	2.99
M055	Aug-00 - Jun-01	55	22.27	11.12	5.97	1.38
M057	Sep-00 - Jun-01	54	19.01	13.10	14.61	2.46
Average		53.6	27.95	19.48	21.96	2.37

^a See text for definition of home-range estimation techniques used.

Home ranges

Plots of cumulative range size reached clear asymptotes (Figure 4.1), with $95.9 \pm 2.8\%$ of final range area achieved after just 40 locations, a total exceeded for all five birds. Estimates of home-range size for the five nightjars monitored for eight months or more are provided in Table 4.2. The 100% MCP ranges averaged 27.95 ± 4.24 ha, whereas estimates based on 95% MCPs were $29.6 \pm 7.8\%$ smaller, highlighting the disproportionate influence of a small number of peripheral

fixes on 100% MCP ranges. Although the 95% isopleth from kernel analysis occasionally included unused areas bordering zones of high use (Figure 4.2), the kernel range estimates (95% KER) broadly coincided with those provided by MCP methods. The notable exception was M055, where the patchy nature of the utilisation distribution resulted in a kernel range about half the size of the 95% MCP range. The non-uniform utilisation of ranges was further emphasised by the results of 90% cluster analysis (90% CLU), which identified core areas of high usage. The latter averaged 2.37 ± 0.31 ha, or just $8.8 \pm 1.2\%$ of the 100% MCP range area.

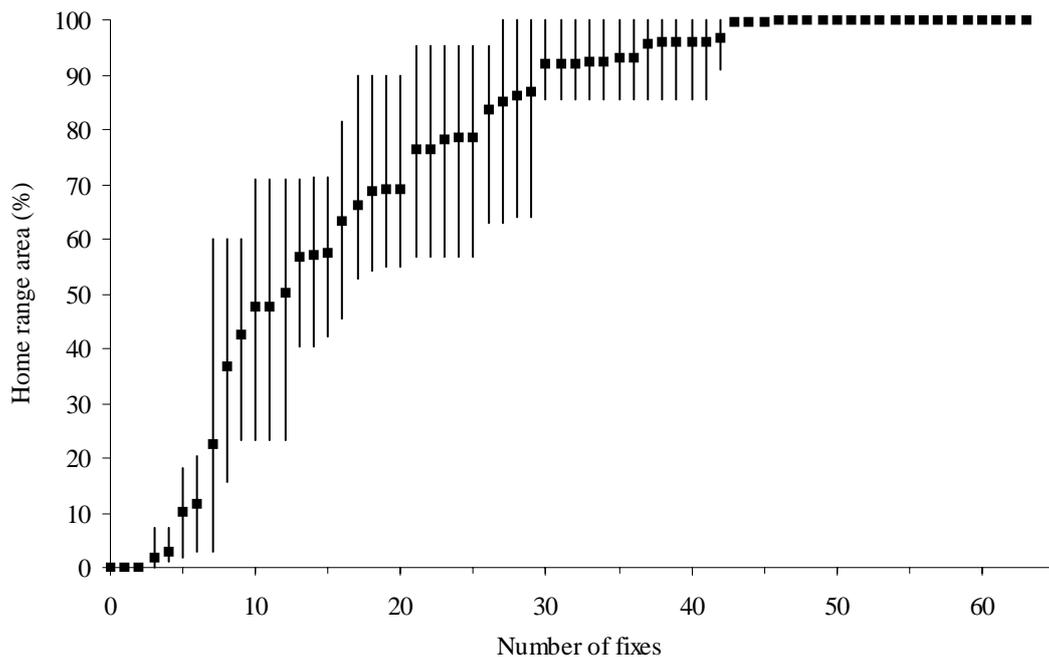


Figure 4.1 Change in 100% MCP range area estimate with number of radio-tracking locations for five nightjars monitored between August 2000 and June 2001. Squares represent means; vertical bars denote individual minimum and maximum values. Locations excluded in random order, as suggested for discontinuous radio-tracking studies (see Methods).

Four of the nightjars monitored had home ranges centred on one ridge and its two adjoining valleys; no other (untagged) individuals were believed to utilise the same area. The extent to which these ranges (as estimated by 100% and 95% MCPs) overlapped varied considerably between individuals (Table 4.3). In general, 100% MCP ranges showed the greatest degree of coincidence, with an average of $21.0 \pm 4.5\%$ overlap between range pairs ($n = 12$). The data suggested minimal overlap between the home ranges of the two females, whereas the ranges of males overlapped to varying extents with each other, and with those of the females (Figure 4.3). The home-range core areas – as identified by 90% cluster analysis – were found to be almost entirely exclusive, with a mean degree of overlap of just $1.5 \pm 0.6\%$ (range: 0.0-5.6%; $n = 12$ range pairs).

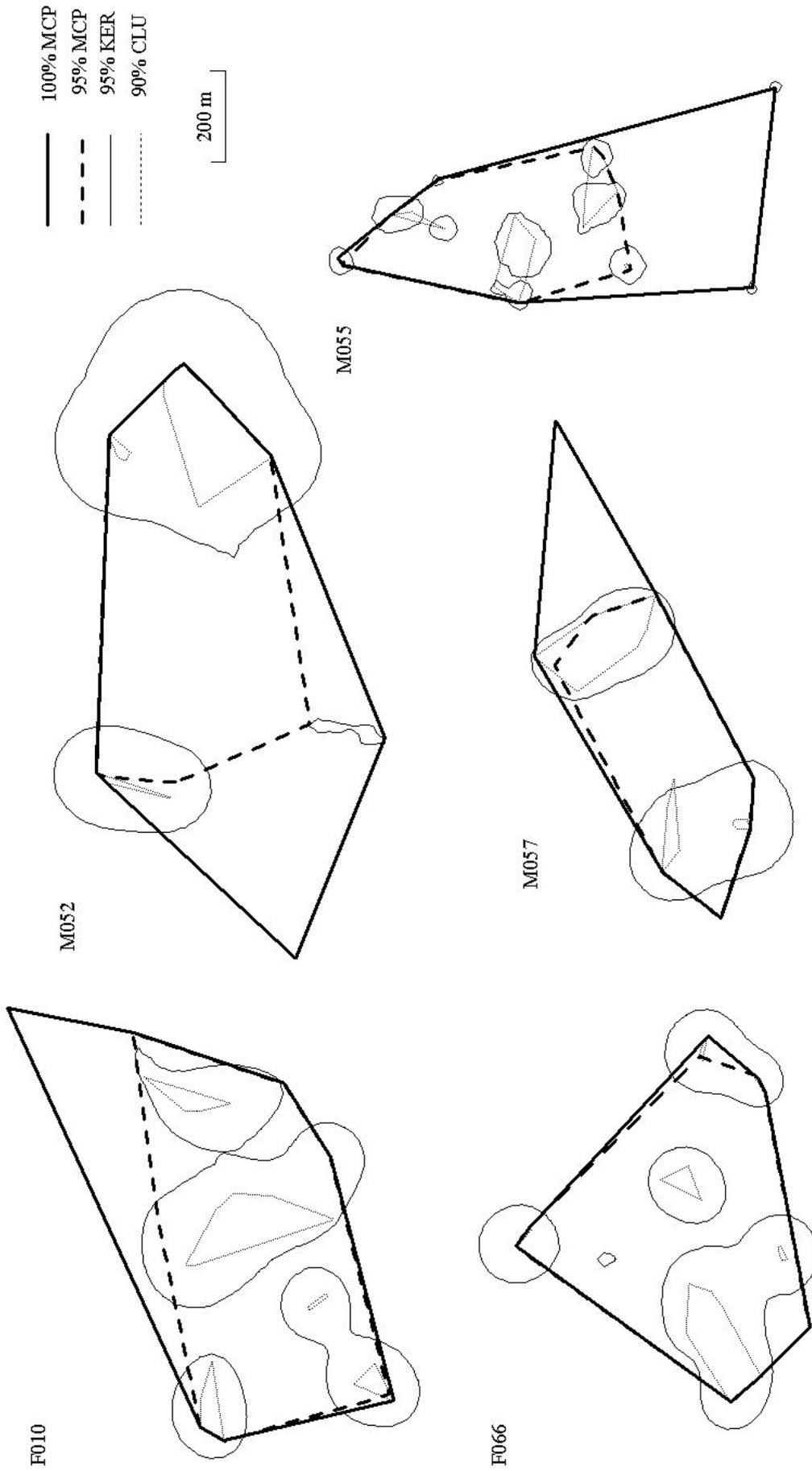
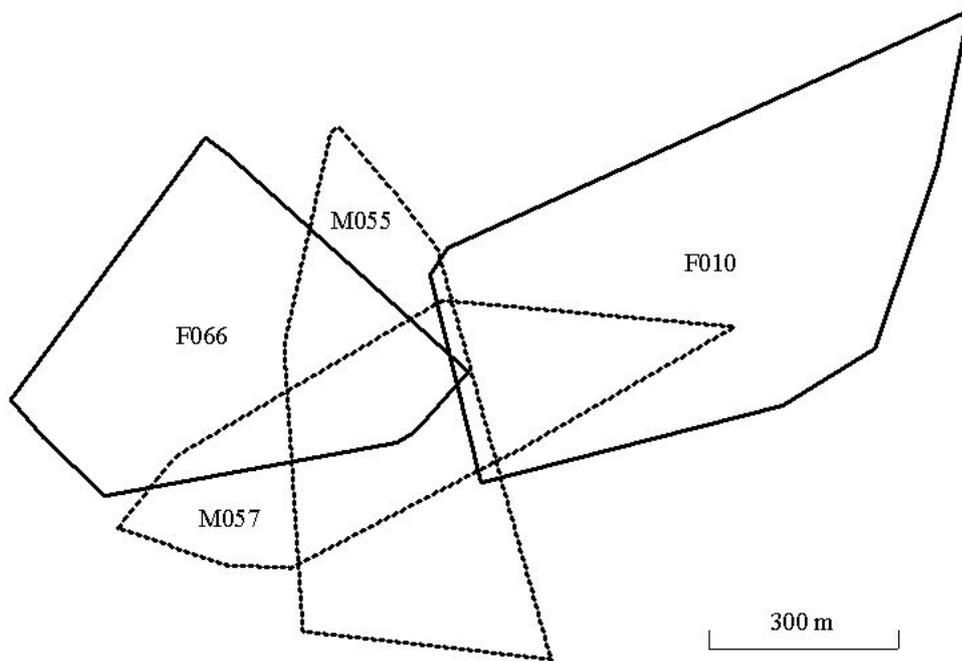


Figure 4.2 Estimates of home-range configuration for two female and three male nightjars monitored between August 2000 and June 2001. Four methods of home-range analysis presented: 100% minimum convex polygons (100% MCP); 95% peeled polygons (95% MCP); 95% kernel isopleth (95% KER); 90% clusters (90% CLU). Home ranges drawn to same scale but spatially separated for clarity.

Table 4.3 Extent of overlap between home ranges of four neighbouring nightjars. Percentage of 100% MCP (95% MCP) range of individual in row overlapped by that of individual in column.

Individual	F010	F066	M055	M057
F010	–	0.2 (0.0)	3.1 (1.3)	19.0 (4.2)
F066	0.3 (0.0)	–	28.1 (24.5)	23.4 (20.0)
M055	4.8 (3.4)	28.2 (48.3)	–	38.2 (42.5)
M057	34.0 (8.0)	28.0 (33.7)	44.9 (36.1)	–

(a)



(b)

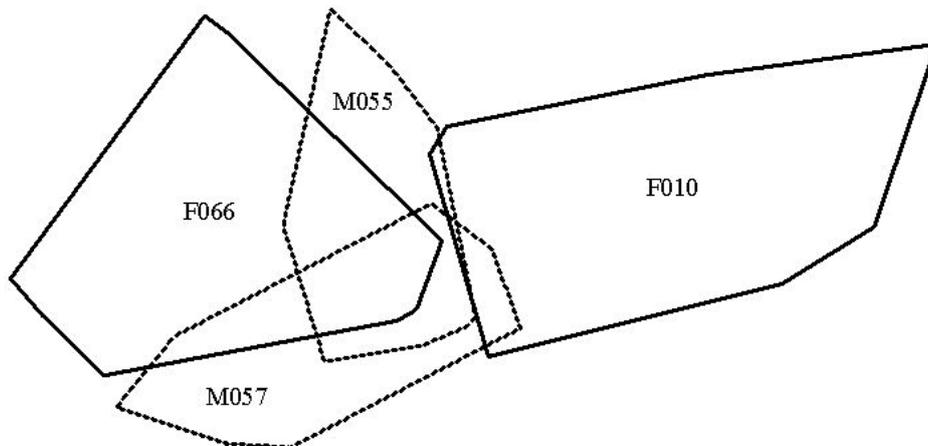


Figure 4.3 Schematic representation of home-range overlap for four neighbouring nightjars monitored between August 2000 and June 2001, as estimated by: a) 100% MCPs; b) 95% MCPs.

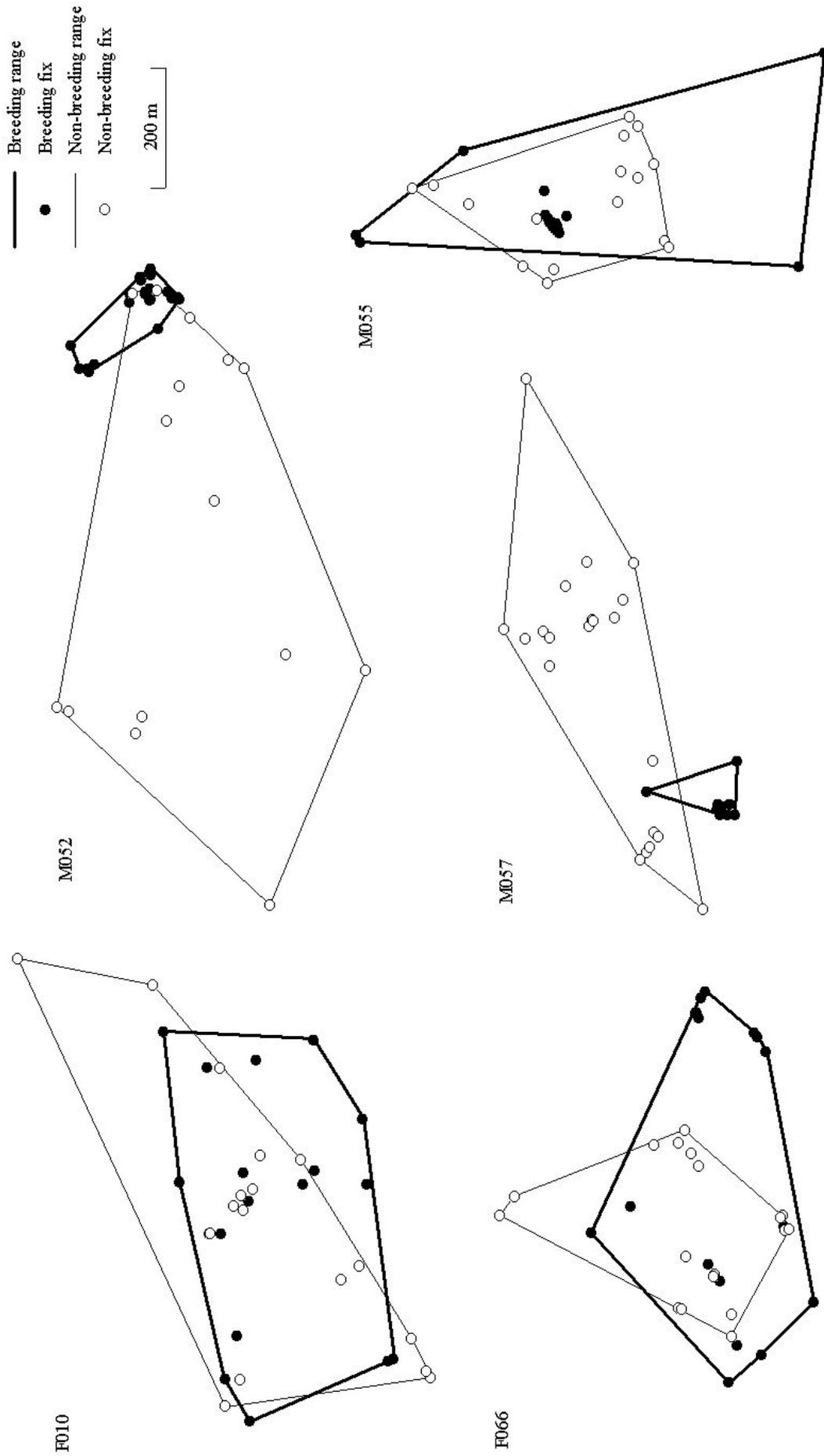


Figure 4.4 Size and relative location of breeding (August–December 2000) and non-breeding (February–June 2001) home ranges of two female and three male nightjars, as estimated by 100% minimum convex polygons.

To investigate any potential seasonal variation, estimates were made of range size during the breeding (August to December) and non-breeding (February to June) seasons, using the 100% MCP method, for the five nightjars monitored for eight or more months. There was no significant difference between the size of breeding and non-breeding ranges (12.19 ± 4.52 ha *versus* 19.44 ± 5.42 ha; paired *t*-test: $t_4 = -0.87$, $P > 0.05$), with considerable variation apparent amongst individuals (Figure 4.4). Although the number of locations per seasonal range varied between 21-33, the variation in area was not attributable to differences in sample size (Spearman rank correlation: $r_s = -0.56$, $n = 10$, $P > 0.05$). When data for the breeding-season ranges of four additional individuals were included in the analysis, there was still no significant difference in mean range size by season (unpaired *t*-test: $t_{12} = -0.93$, $P > 0.05$).

In general, male nightjars rarely ventured far from their ‘display arenas’ (see Chapter 3) during the breeding season. Males were located up to 760 m away from display arenas on occasions, but almost 97% of nocturnal breeding-season fixes fell within 150 m of their relevant arenas (average: 41.5 ± 10.0 m, $n = 146$ fixes from seven males; Figure 4.5). A small number of more distant locations had a disproportionate effect on the size of the breeding range of some individuals, but four males (including M057 and M052; see Figure 4.4) used breeding ranges of less than two hectares.

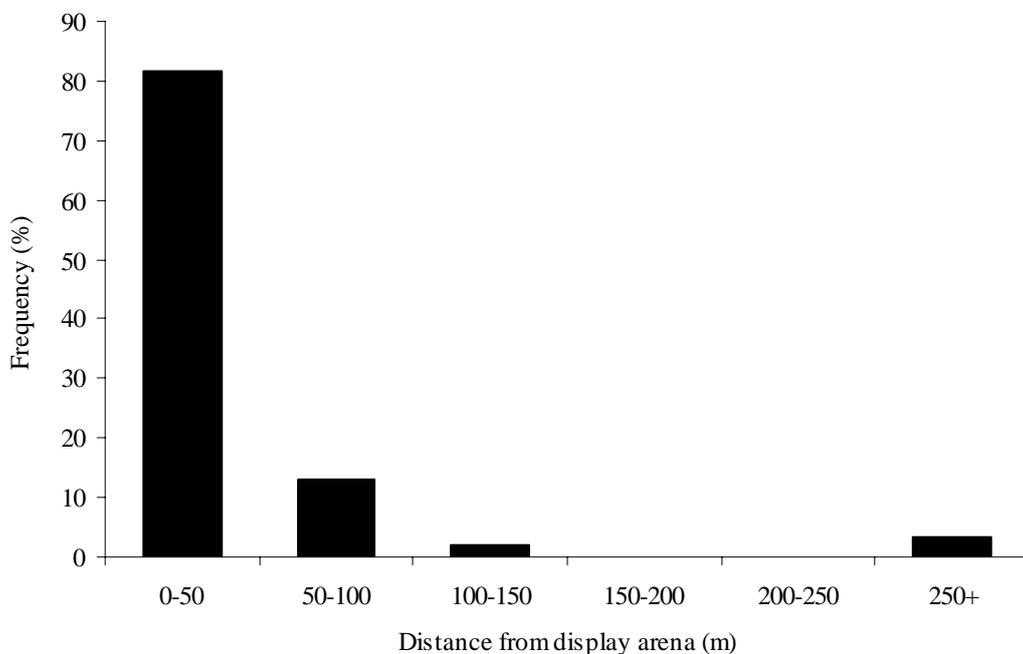


Figure 4.5 Frequency distribution of nocturnal radio-tracking locations ($n = 146$) in relation to display arena for seven male nightjars monitored during 2000 breeding season (August-December).

Habitat use

Figure 4.6 shows the habitat composition of the study area and home ranges (as defined by 100% MCPs) of five nightjars monitored between August 2000 and June 2001. Compared to the whole study area, nightjar home ranges contained on average more ‘campo cerrado (00)’ and ‘campo cerrado (99)’, and less ‘campo cerrado (97)’, ‘wet grassland’ and ‘forest’ (Table 4.4). There was considerable variation between individuals in home-range composition, but each range contained on average 2.4 ± 0.2 habitat categories. ‘Campo cerrado (99)’ was the only habitat category to occur in every home range (comprising $> 50\%$ of each), whereas ‘campo cerrado (97)’ and ‘forest’ were absent from all five.

Table 4.4 Habitat composition of the home ranges (100% MCPs) of five radio-tagged nightjars monitored between August 2000 and June 2001 in relation to the study area as a whole.

Habitat category	Composition of study area (%)	Composition of home ranges (%)					
		Mean \pm se	F010	F066	M052	M055	M057
Campo cerrado (97)	10.3	0.0	0.0	0.0	0.0	0.0	0.0
Campo cerrado (99)	68.2	82.4 ± 5.8	66.5	75.7	94.9	96.3	78.5
Campo cerrado (00)	1.8	4.7 ± 3.1	0.0	3.1	0.0	3.7	16.8
Wet grassland	18.8	12.9 ± 6.3	33.5	21.2	5.1	0.0	4.7
Forest	0.9	0.0	0.0	0.0	0.0	0.0	0.0

Within their home ranges, overall nightjar habitat use differed from random, both when foraging (G -test: $G = 7.83$, $df = 2$, $P < 0.05$) and roosting ($G = 7.35$, $df = 2$, $P < 0.05$; Table 4.5, Figure 4.7a). However, when simultaneous confidence intervals were calculated for habitats individually, only the avoidance of ‘campo cerrado (99)’ by foraging nightjars was found to be significant. Nonetheless, as breeding-season habitat usage may have been constrained by ranging behaviour (see above), non-breeding habitat use was also inspected separately. Non-breeding ranges were on average $74.2 \pm 7.4\%$ the size of overall home ranges, but did not differ significantly in their habitat composition (paired t -tests: $P > 0.1$ for all habitats). The distribution of foraging fixes within non-breeding ranges did, however, differ significantly from random ($G = 24.86$, $df = 2$, $P < 0.001$, $n = 108$ fixes; Figure 4.7b), with simultaneous confidence intervals showing that nightjars preferred ‘campo cerrado (00)’ and avoided ‘campo cerrado (99)’ vegetation when foraging. Figure 4.8 demonstrates that these patterns of habitat selection were largely consistent at the individual level. Although data were too few for valid application of the G -test, nightjars also appeared to avoid older, and prefer younger, campo cerrado vegetation when selecting roost sites during the non-breeding season (Figure 4.7b).

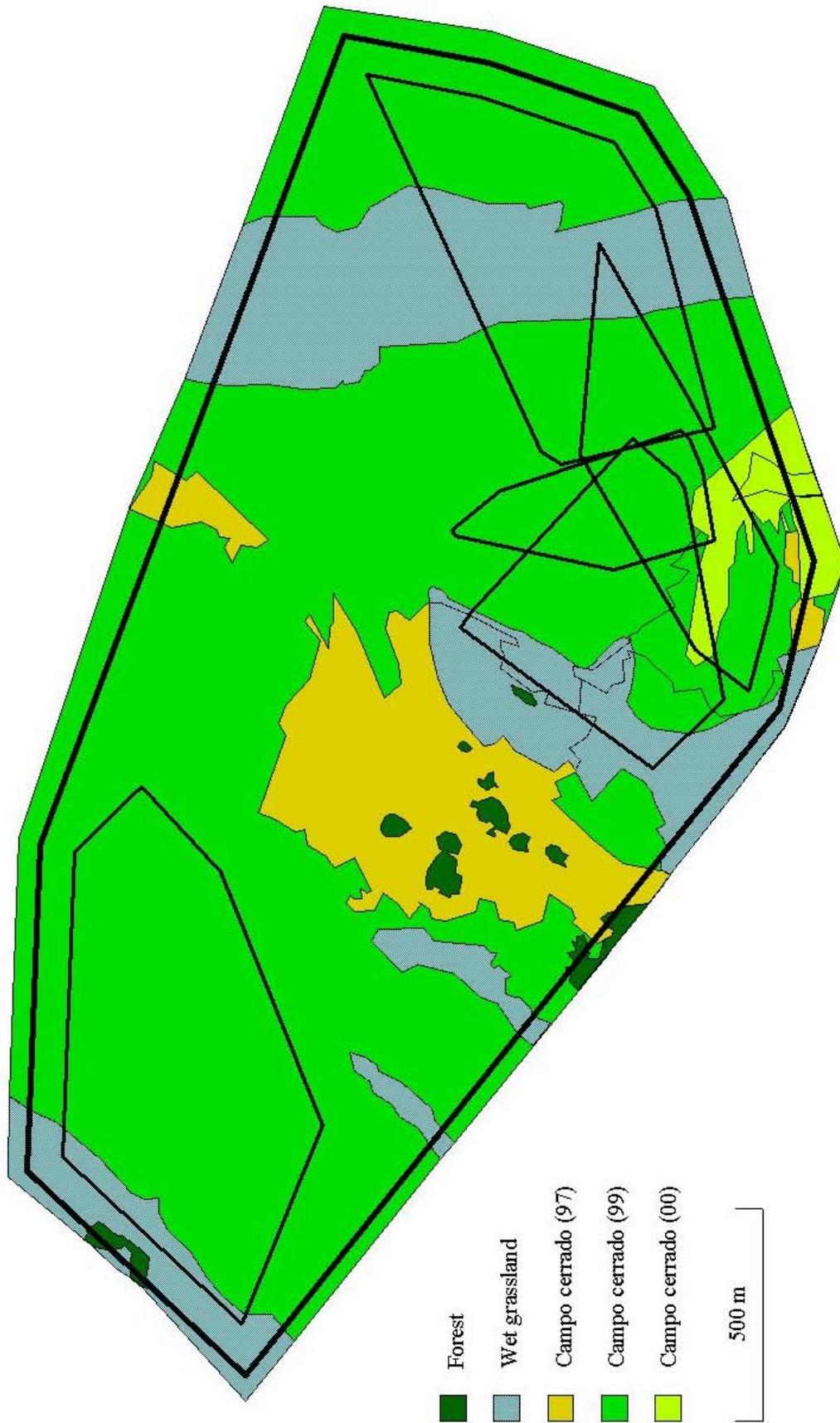


Figure 4.6 Habitat composition of radio-tracking 'study area' (heavy black line) and 100% MCP home ranges of five nightjars monitored between August 2000 and June 2001.

Table 4.5 Habitat use of five radio-tagged nightjars between August 2000 and June 2001 in comparison to that expected from the composition of their home ranges (100% MCPs).

Habitat category	No. (%) of foraging fixes ($n=187$)		No. (%) of roost fixes ($n=28$) ^a	
	Expected ^b	Observed	Expected ^b	Observed
Campo cerrado (99)	155.4 (83.1)	141 (75.4)	23.1 (82.7)	18 (64.2)
Campo cerrado (00)	8.5 (4.5)	15 (8.0)	1.4 (4.9)	5 (17.9)
Wet grassland	23.1 (12.4)	31 (16.6)	3.5 (12.4)	5 (17.9)

^a Includes three roost sites that were subsequently also used as nests.

^b Values calculated from habitat composition of individual home ranges (weighted for number of fixes).

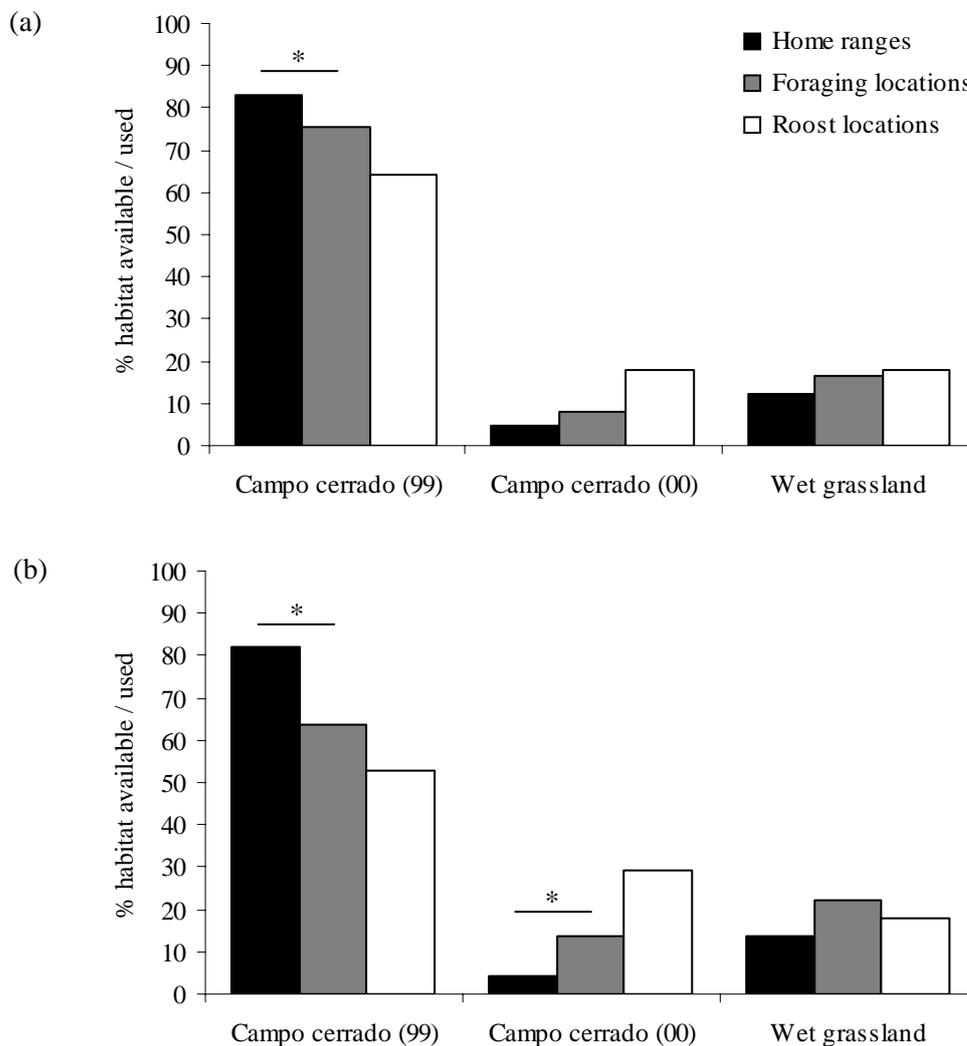


Figure 4.7 Comparison of habitat composition of mean home range *versus* radio-telemetry locations for five nightjars monitored between August 2000 and June 2001: (a) foraging ($n=187$) and roosting ($n=28$) fixes for whole tracking period; (b) foraging ($n=108$) and roosting ($n=17$) fixes from non-breeding season only (February to June 2001). Asterisks denote differences significant with simultaneous confidence intervals. Note: 'campo cerrado (97)' and 'forest' habitats absent from all ranges (see Table 4.4).

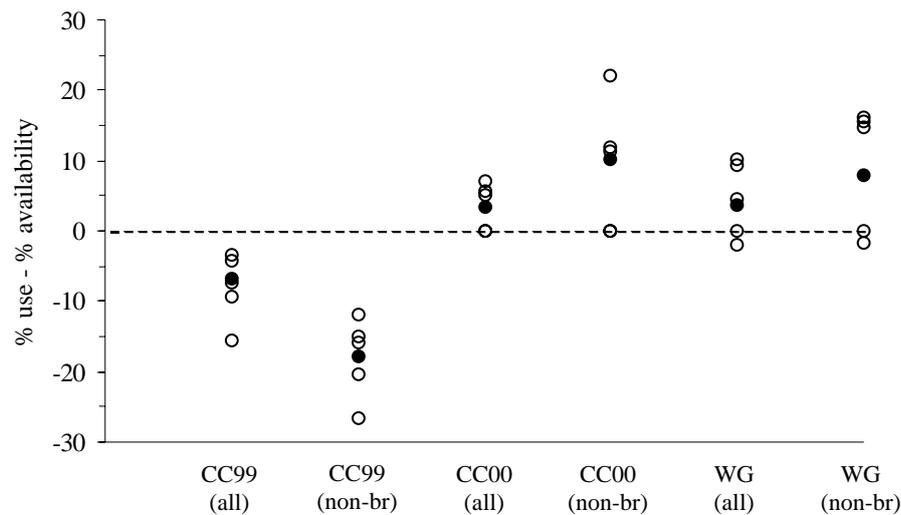


Figure 4.8 Individual variability in habitat selection for five nightjars monitored between August 2000 and June 2001. Individual values (open circles) and mean values (filled circles) plotted. Points above line indicate some preference for habitat; points below line indicate some avoidance. Data provided separately for whole tracking period ('all') and non-breeding season only ('non-br'). 'CC99' = 'campo cerrado (99)'; 'CC00' = 'campo cerrado (00)'; 'WG' = 'wet grassland'. Values of zero provided for CC(00) and WG for individuals without these habitats in their home ranges.

The ranging behaviour and habitat use of three nightjars (M055, M057 and F066) were monitored for eight weeks immediately following the experimental burn of 10 July 2001. During this period, an average of 13.7 ± 1.2 foraging fixes was obtained for each individual, and the distribution of these fixes in relation to the availability of newly burnt habitat is summarised in Table 4.6. When data were pooled across individuals, the distribution of foraging fixes differed from random in a highly significant fashion (G -test: $G = 12.74$, $df = 1$, $P < 0.001$). Nightjars apparently avoided the newly burnt habitat, with just two foraging fixes obtained from the burn parcel during the first month following the fire. The remaining four burn fixes were obtained for M055 during the second half of August, and were subsequently confirmed to fall in close proximity to the male's display arena. For all three individuals, the proportion of foraging fixes falling within the burn parcel was lower in the two months immediately following the fire (Figure 4.9).

Table 4.6 Distribution of foraging fixes for three nightjars over the eight weeks following an experimental burn partially overlapping with their home ranges.

Individual	Total no. of foraging fixes	No. (%) of fixes in burn	Expected no. (%) of fixes in burn ^a
M055	12	5 (41.7)	5.45 (45.4)
M057	13	1 (7.7)	8.97 (69.0)
F066	16	0 (0)	4.39 (13.2)
Pooled	41	6 (14.6)	16.53 (40.3)

^a Based on proportion of individual's post-fire 100% MCP range affected by burn.

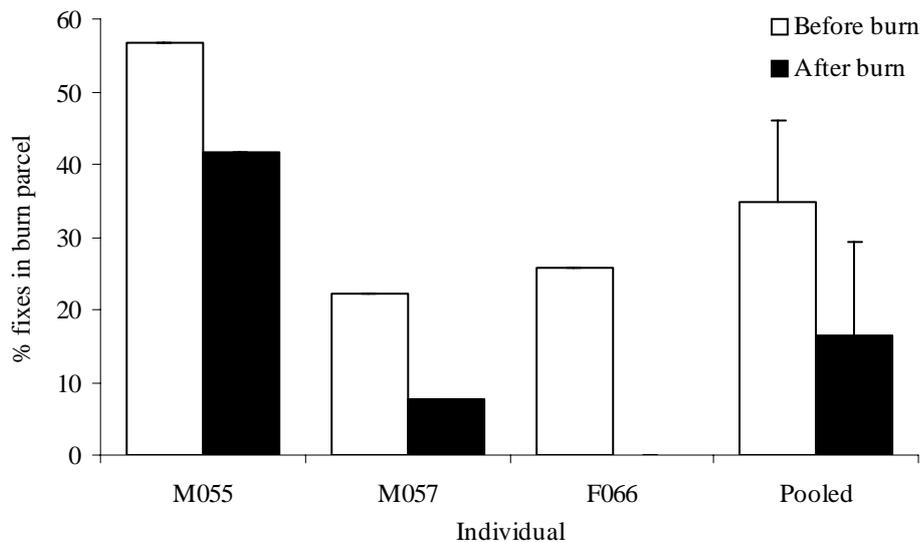


Figure 4.9 Proportion of foraging fixes for three nightjars falling within designated burn parcel before, and during eight weeks following, an experimental burn.

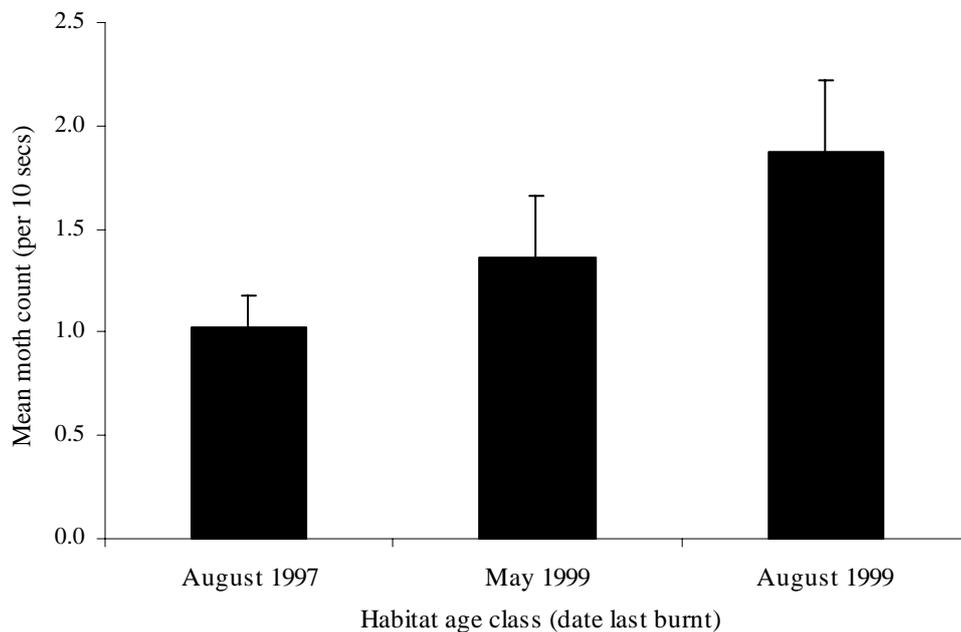
Feeding ecology

Although it was never confirmed visually, the signal noted from radio-tagged nightjars at dusk strongly supported the suggestion that they spent several minutes hawking insects in continuous flight after leaving their roost sites. However, following the change to a ‘sit-and-wait’ strategy, four nightjars sallied at variable rates of 0.07-1.42 sallies per minute (mean: 0.67 ± 0.18 ; data from 750 mins observation over six nights). Too few data were obtained to carry out a rigorous analysis of potential correlates of foraging rate, but general observations suggested that, whilst particularly high in the first two hours after sunset, sallying activity continued into the night when light conditions permitted. The majority of sallying attempts observed were made for insects flying within one to ten metres of the perch. On the few occasions when prey items could be identified, they included species of Coleoptera, Diptera and Lepidoptera.

Analysis of the moth count data from September to November 1999 suggested that moth abundance was subject to short-term variation in environmental variables: the effects of ‘shift’ and ‘night’ were both highly significant ($P < 0.001$; Table 4.7). Moths were more abundant during early shifts and as the season progressed, but it was not possible to determine whether the latter relationship was due to a seasonal effect, or the result of another confounding variable, such as temperature. Habitat age also showed a significant, albeit marginal, effect ($P = 0.04$), with younger habitats tending to produce higher moth counts than older habitat classes (Figure 4.10). Neither habitat type nor the habitat type-age interaction term had any significant effect.

Table 4.7 Summary of an ANOVA explaining variation in moth abundance in six habitat patches of two types and three age classes (see Methods).

Factor	df	<i>F</i>	<i>P</i>
Habitat type	1	0.83	NS
Habitat age	2	3.43	0.04
Type * age	2	2.01	NS
Shift	1	22.93	< 0.001
Night	4	9.48	< 0.001
Error	49		

**Figure 4.10** Relationship between an estimate of moth abundance (mean \pm se) and habitat age. Data from 10-second horizontal beam moth counts conducted during September–November 1999.

Roosting behaviour

In total, 78 roost sites of 17 radio-tagged nightjars were identified between 1998 and 2001. Of these, 92% were located in ‘campo cerrado’ habitat, and 8% in ‘wet grassland’ (all within 50 m of the habitat boundary with campo cerrado). Roost sites occurred in habitats that had burnt between two and twenty-eight months earlier, but in many circumstances (e.g. after major burns) individuals were severely constrained by the limited range of habitat age classes available to them. The burn of 7 October 2000 partially overlapped with the home ranges of three individuals, but none of these was confirmed to roost in the burnt area until at least six months after the fire.

Preliminary analysis using univariate tests suggested that the vegetation characteristics of roost sites differed significantly from random sites in two variables (Table 4.8). However, a binary logistic regression model, explaining 59% of the deviance in site use, showed ‘bare ground cover’

to be the only significant predictor of site use (Table 4.9): on average, roost sites had more than six times the amount of bare ground than random sites. The model correctly reclassified 87.5% of sites overall, with a roughly equal degree of reclassification success for roost and random sites.

Table 4.8 Mean values (\pm se) of vegetation variables for roost sites used by nightjars between February and May 2001 and an equal number of random sites.

Variable	Roost site ($n = 12$)	Random site ($n = 12$)	Significance ^a
Grass cover (%)	40.4 \pm 7.3	57.4 \pm 5.7	$W = 177$, NS
Herbaceous cover (%)	21.4 \pm 5.1	34.6 \pm 5.9	$W = 179$, NS
Shrub/sapling cover (%)	4.1 \pm 2.8	0.3 \pm 0.1	$W = 147$, NS
Bare ground cover (%)	22.9 \pm 4.5	3.6 \pm 1.4	$W = 84$, $P < 0.001$
Grass height (cm)	98.2 \pm 14.3	122.9 \pm 13.8	$W = 188$, $P = 0.03$
Herb height (cm)	33.5 \pm 3.8	46.7 \pm 4.7	$W = 201$, $P = 0.004$
Shrub/sapling height (cm)	9.6 \pm 5.0	9.3 \pm 5.2	$W = 146$, NS
Overhead cover (%)	50.8 \pm 8.0	40.8 \pm 6.4	$W = 138$, NS
No. of saplings	0.9 \pm 0.3	1.9 \pm 0.6	$W = 172$, NS
No. of yata'i	0.6 \pm 0.4	0.4 \pm 0.4	$W = 139$, NS
Yatai density (ha^{-1})	61.9 \pm 10.1	73.6 \pm 11.7	$W = 162$, NS

^a From Mann-Whitney U -tests. Values underlined indicate table-wide significance at an adjusted initial α level of 0.0045 (Rice 1989).

Table 4.9 Summary of the model discriminating between nightjar roost sites ($n = 12$) and an equal number of random points.

Variable	Coefficient	SE	% correctly reclassified ^a	% of deviance explained ^b	χ^2	df	P
Intercept	-3.045	1.167					
Bare ground cover	0.305	0.107	87.5	59.3	19.74	1	< 0.001

^a Percentage of points correctly reclassified by the model as roost sites ($P > 0.5$) or random ($P < 0.5$).

^b Total deviance = 33.3; residual deviance = 13.5.

Roosting nightjars typically faced onto a small area of bare ground (mean dimensions: 47 \pm 6 cm by 33 \pm 5 cm; $n = 19$), which acted as a 'runway' from which they took off and landed. The orientation of roosting birds did not differ significantly from random (G -test: $G = 3.03$, $df = 3$, $P > 0.05$; $n = 44$), and on occasions individuals changed their orientation during the course of the day. Nightjars typically left their roost sites 25 to 30 minutes after sunset, i.e. shortly following the end of civil twilight, and were not believed to return until just before dawn. However, on seven nights during May and June 2001, radio-tagged nightjars were found inactive at daytime roost sites one to six hours after sunset. Nights on which this was observed were significantly colder on average than ten nights during May and June when radio-tagged birds were found to be active as

usual (minimum night-time temperature: 8.2 ± 1.5 °C versus 15.7 ± 0.9 °C; unpaired *t*-test: $t_{15} = -4.42$, $P < 0.001$). Birds were extremely reluctant to flush on all such occasions, suggesting they may have been in torpor, although on two nights transmitter signals indicated that the individuals had been active earlier in the evening.

Nightjars relied extensively on their cryptic plumage when roosting, often remaining motionless, with eyes closed to slits, until an observer approached to within one metre or less. When alarmed, however, birds moved forward onto the 'runway', from which they could take off unimpeded. Occasionally, individuals performed a presumed threat display: puffing up the contour feathers, fanning the tail and drooping the wings, whilst raising the head and neck and/or wagging the body from side-to-side. An extreme version of the display was observed on two occasions, when the wing furthest from the observer was held, fully open, vertically over the bird's back. When flushed, birds flew 5 to 35 metres before dropping to the ground in a clumsy manner.

DISCUSSION

White-winged Nightjars in Aguará Ñu utilised home ranges of at least 20 to 40 ha in size during the eight to ten month period over which they were monitored. Few previous studies have attempted to quantify the size of nightjar home ranges using radio-telemetry methods, but one study of European Nightjars *Caprimulgus europaeus* in Switzerland provided similar estimates (23.6-40.4 ha) for the breeding ranges of three males (Sierro *et al.* 2001). In the current study, non-MCP methods of range estimation also highlighted the patchy usage of home ranges by nightjars. For all five individuals, 90% of radio-tracking fixes could be encompassed within three to six 'core areas' occupying just ten percent of the overall range area. Overlap matrices showed that core areas were almost entirely exclusive, whereas MCP range estimates did show some degree of overlap between neighbours.

No evidence was obtained to suggest that nightjars were migratory: five birds monitored continuously for eight to ten months remained faithful to the same area throughout. The home ranges of two female nightjars varied little in size or location between the breeding and non-breeding season, whereas males showed more variable patterns of ranging. During the breeding season, males rarely ventured farther than 100 m from display arenas, resulting in very restricted estimates of breeding-range size (of less than 2 ha) for some birds. The breeding ranges of two males were noticeably peripheral to the areas that they used during the non-breeding season, lending support to the suggestion that male display territories may be located partly on the basis of extrinsic, perhaps topographical or historical, factors (Chapter 3).

Although the habitat composition of nightjar home ranges differed from that of the study area as a whole, the uneven distribution of habitats meant that individuals were unlikely to have had equal access to all habitats. Problems of habitat availability are inherent in second-order or ‘used *versus* unused’ comparisons, and any apparent avoidance of habitats should be interpreted with caution (Jones 2001). Nevertheless, qualitative observations of the spatial distribution of caprimulgids at Aguará Ñu suggest some partitioning of habitats between species (see also Rodrigues *et al.* 1999). White-winged Nightjars were only recorded from campo cerrado and wet grassland habitats, apparently sharing the latter with Spot-tailed Nightjars *Caprimulgus maculicaudus*. It was not possible to quantify the structural density of campo cerrado habitats during the current study, but observations suggested that the study species avoided areas of high palm density, with these areas of ‘palm savanna’ apparently preferred by Little Nightjars *C. parvulus*. White-winged Nightjars were never recorded from gallery forest or isolated stands of forest, which were used primarily by Rufous Nightjars *C. rufus* and Pauraques *Nyctidromus albicollis* respectively.

At a finer scale, White-winged Nightjars did show significant patterns of habitat selection when choosing foraging sites within their home ranges. The observed avoidance of older, and preference for younger, campo cerrado vegetation was particularly apparent during the non-breeding season, and although a similar pattern was evident within the overall data set, it may have been tempered by the restricted ranging behaviour of some individuals during the breeding season. Various authors have suggested that White-winged Nightjars show a preference for younger vegetation (e.g. Collar *et al.* 1992, Lowen *et al.* 1997, Rodrigues *et al.* 1999), but this represents the first study in which such an affinity has been confirmed in a quantifiable manner.

The selection of foraging habitats by birds is influenced by a number of factors, including inter- and intra-specific competition, predation risk and food availability (Cody 1985a, Vickery *et al.* 1999). In the current study, some evidence was obtained to suggest that White-winged Nightjars selected habitats on the basis of food availability. Most nightjar species feed on flying insects, especially moths and beetles (see Cramp 1985, Bayne & Brigham 1995, Jackson 2000a,b, Siervo *et al.* 2001), and the limited evidence available for the study species suggests it is no exception. The stomach of an injured male collected in 1997 (Capper *et al.* 2000) contained winged insects of various orders (Coleoptera, Diptera, Heteroptera, Hymenoptera and Lepidoptera), with moths the most abundant (B. Garcete Barrett *in litt.* to R. P. Clay 1997). Although climatic conditions were found to be by far the most significant factor affecting moth abundance in the current study (see also Kunz 1988, Csada & Brigham 1994, Yela & Holyoak 1997), habitat age also showed a significant effect when controlling for the former. This finding supports the suggestion that nightjars may benefit from the abundant insect prey attracted to vegetation regrowing after fires (Rodrigues *et al.* 1999). The cerrado flora is adapted to wildfires and regrows rapidly after burns

(Coutinho 1982, Ratter *et al.* 1997, Mistry 1998), but it took four to eight weeks for a semi-complete cover of herbs and grasses to regrow in Aguará Ñu (see Plate 4.1). During the interim period, laying sites, cover and food for insect prey were all limited, potentially explaining why nightjars significantly avoided burnt habitats for at least two months following the experimental burn in this study.

Food availability is determined not only by prey abundance but also by its accessibility, and various studies of open country birds have emphasised the influence of vegetation structure on foraging behaviour (reviewed in Cody 1985b). Since nightjars detect their flying prey visually, their foraging activity is constrained both by ambient light levels (Brigham & Barclay 1992, Cresswell & Alexander 1992, Bayne & Brigham 1995) and by the structure of the surrounding vegetation. Where possible, the study species used perches of similar height to that of the local vegetation (*pers obs.*, Capper *et al.* 2000), but under some circumstances habitat structure did still impose some constraints on sallying. During December 2000 and January 2001, flowering grass stems, 1.5-2.5 m tall, grew up in many areas of ‘campo cerrado (99)’ vegetation at Aguará Ñu (Chapter 1; see also Plate 4.2), dramatically changing the habitat structure. This may partly explain why foraging nightjars avoided this habitat category during the 2000/1 non-breeding season (February to June 2001).

Most nightjar species roost and nest directly on the ground, and their cryptic variegated plumages have evolved to minimise the risk of detection by diurnal predators (Cleere 1998, Holyoak 2001). Male White-winged Nightjar have the most extensive white markings of any species in the family (Chapter 5), but even these are almost entirely concealed when the bird is at rest, as predicted by the ‘restricted signalling strategy’ (Aragonés *et al.* 1999). Nevertheless, the plumage of the study species is not as closely matched to its environment as that of certain other species (see Plate 4.2, *cf.* photos on pp. 306-307 in Cleere 1999), and birds also required some vegetation cover at roost sites. Whilst nightjars did roost in habitats as young as two months, they avoided habitats burnt within the preceding six months when older habitats were available. However, there was an apparent trade-off between vegetation cover and access, as demonstrated by the need for a bare ‘runway’ at roosts, also noted in a study of Common Poorwill *Phalaenoptilus nuttallii* roost sites (Wang & Brigham 1997). The decreased availability of suitable clearings in more dense habitats might explain why roosting nightjars showed a tendency to avoid older campo cerrado habitats in the current study.

Physiological studies of free-ranging Common Poorwills have shown that they regularly enter torpor on cold nights (particularly during the non-breeding season), when their insect prey are less abundant (Brigham 1992, Csada & Brigham 1994). Conclusions based solely on behavioural

observations (e.g. Santos Moraes & Krul 1995) should be treated cautiously, but the discovery of nightjars inactive at roosts on various nights in May and June during the current study suggested that White-winged Nightjars may also enter torpor on occasions. Common Poorwills forage actively at dusk on all nights, potentially using the ambient temperature at the end of twilight as a cue whether to enter torpor or not (Brigham 1992). Night-time temperatures in Aguará Ñu dropped as low as -2 °C during the current study (unpubl. data), and it was interesting that nightjars were more commonly found inactive at their roost sites on colder nights. Anecdotal evidence also suggested that nightjars used roost clearings for thermoregulatory purposes, potentially rewarming themselves in the sun after bouts of torpor (see also Wang & Brigham 1997).

CONCLUSIONS

Using radio-telemetry, this chapter has provided the first detailed description of the ranging behaviour and habitat preferences of the White-winged Nightjar. The size, configuration and overlap of nightjar home ranges are documented for the first time, using a number of analytical techniques, and during both the breeding and non-breeding seasons. Habitat use by nightjars was inspected at two spatial scales and functional explanations were provided for observed departures from random usage. The practical implications of the chapter's findings for the conservation of the species and the management of the study site are discussed further in Chapter 6. In the meantime, the focus shifts away from fieldwork in Chapter 5, as the signalling strategy, plumage and mating system of the study species are put in the context of the family Caprimulgidae as a whole.

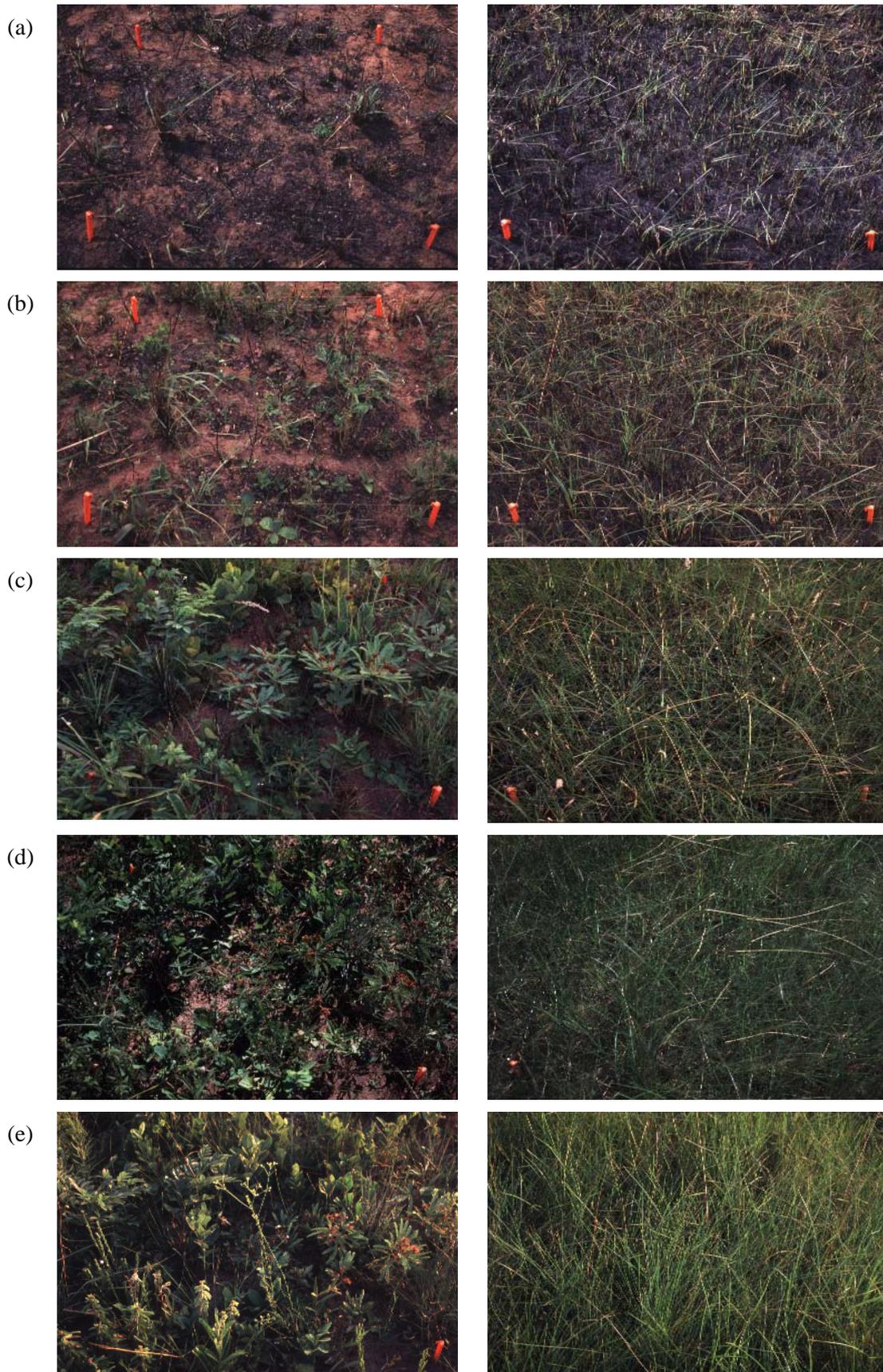


Plate 4.1 Regrowth of campo cerrado (left) and wet grassland (right) vegetation following a natural burn during August 1999. Photos taken: (a) 15; (b) 30; (c) 60; (d) 90; (e) 120 days after the burn.



(a)



(b)



(c)



(d)

Plate 4.2 Habitat use: (a) aerial photo of study site showing wet grassland habitat of valley bottoms and campo cerrado of ridgelines; (b) tall flowering stems of *Loudetia flammida* atop old campo cerrado vegetation. Roosting behaviour: (c) typical roost site in campo cerrado; (d) male nighthawk at roost.

CHAPTER 5

WHITE PLUMAGE MARKINGS AND SEXUAL DIMORPHISM IN THE CAPRIMULGIDAE

SUMMARY

This chapter presents the first quantitative analysis of size and plumage dimorphism in the family Caprimulgidae. The extent of white markings in the wings, tail and throat was scored for 521 museum specimens of 66 nightjar species. White scores were obtained from adult male and female specimens, and a categorical assessment of dimorphism in white was provided for each species. Sufficient information was available in the literature to derive white scores for a further seven species, so overall 73 nightjar species were assessed for white dimorphism. Across all species, the male White-winged Nightjar scored highest for ‘overall’ (wing and tail combined) white, although it showed no white on the throat. The female, meanwhile, was one of 28 (38%) species that lacked white wing and tail markings entirely. Although 58 (79%) of the species assessed showed some sexual dimorphism in wing or tail white, the White-winged Nightjar was by far the most extreme in absolute terms. In all cases, the male was the whiter sex. When considering wing and tail white separately, sexual dimorphism was significantly more common for tail markings than wing markings. Males had significantly whiter, and females less white, tails in species dimorphic for tail white than in their monomorphic counterparts. When the structural density of species’ breeding habitats was investigated, a relationship was found between overall white score and habitat density for both male and female nightjars. This was due to a strong negative correlation between habitat density and wing white; no such relationship existed with tail white. Species of more open habitats (most notably the study species) had whiter wings, potentially because of the better long-range visibility and possibilities for flight displays. In contrast to the high levels of plumage dimorphism shown for the family, only 10 (14%) species assessed showed any sexual size dimorphism, as defined as a difference of $\geq 10\%$ between male and female measures of wing or tail length. There was no significant association between the occurrence of size and white dimorphism across all 73 species, supporting the suggestion that these two broad classes of dimorphism correlate with different aspects of social and reproductive behaviour. The limited data available on the allocation of parental duties between the sexes suggested that confirmed biparental carers were significantly less likely to display size dimorphism than the remaining, unclassified species. Although the data available on phylogenetic relationships within the family was extremely limited, the most parsimonious interpretation of the results suggested that the ancestral caprimulgid was socially monogamous, sexually dimorphic for white plumage and monomorphic for size.

INTRODUCTION

In addition to its physiological functions, the plumage of birds plays an important role in inter- and intraspecific communication (Savalli 1995, Brooke 1998). As with other animal signals, the evolution of plumage markings has been influenced by a number of factors, including the physical properties of the signalling environment (Endler 1978, Gerhardt 1983, Marchetti 1993, Endler & Théry 1996), the sensory capabilities of the receiver (Krebs & Dawkins 1984, Guilford & Dawkins 1991, Endler 1992), and the function of the signal itself. The use of plumage in interspecific communication is most commonly observed in the context of predator avoidance (e.g. crypsis, confusion effects, predator deflection or mimicry; review in Savalli 1995) or foraging behaviours (e.g. Hailman 1960, Götmark 1987). Intraspecific signals, meanwhile, often relate to reproductive behaviour, in particular displays for the purpose of mate attraction (e.g. Andersson 1982, Møller 1988, Petrie *et al.* 1991), and signals of threat and status to potential competitors (e.g. Smith 1972, Rohwer 1977). In many cases, a conflict may arise between the opposing forces of sexual selection, acting on conspicuous intraspecific signals, and natural selection, favouring concealment from predators or prey (Butcher & Rohwer 1989).

In the Caprimulgidae, or true nightjars, a balance between conspicuousness and crypsis is achieved through the use of a ‘restricted signalling strategy’ (Aragonés *et al.* 1999). As a largely nocturnal family, nightjars rely on their cryptic plumage to avoid detection by predators when at their daytime roosts. Males and females rarely demonstrate significant sexual differences in their camouflaged contour plumages, which often show remarkable coincidence with the local environment (see Cleere 1999). Nevertheless, many species do have white markings in the wings, tail or throat, which are exposed for the purposes of communication in certain behavioural contexts (Mengel 1972, Bruce 1973, Cramp 1985, Clay *et al.* 2000), but are concealed when at rest. The extent of these markings varies considerably within the family, from species like the Brown Nightjar *Caprimulgus binotatus*, with almost no white in the plumage, to the male White-winged Nightjar, in which much of the wing and the four outer pairs of rectrices are white. Relatively few studies have investigated age or sex variation in nightjar markings (Ingels & Ribot 1982, Forero *et al.* 1995, Forero & Tella 1997, Aragonés *et al.* 1999; Chapter 2), but most species display some sexual dimorphism in the amount of white in their plumage (Cleere 1998, Holyoak 2001).

Sexual dimorphism takes a variety of forms in birds, with variation in its extent traditionally attributed to differences in social mating system and parental care (reviews in Butcher & Rohwer 1989, Andersson 1994). In general, however, two broad classes of sexual dimorphism can be distinguished – size dimorphism and plumage-colour dimorphism – each of which typically correlates with a different aspect of reproductive and social behaviour (Owens & Hartley 1998). Size dimorphism is often associated with polygamy and high levels of intra-sexual competition,

though whether the latter occurs on the ground or in the air is of relevance (Payne 1984, Höglund 1989, Owens & Hartley 1998, Székely *et al.* 2000). Plumage dimorphism, meanwhile, has been associated with sexual differences in parental care (e.g. Martin & Badyaev 1996, Bleiweiss 1997) or high levels of extra-pair paternity (Møller & Birkhead 1994), with the relative importance of the two depending upon the type of pigmentation involved (Owens & Hartley 1998).

In this chapter, I present the results of the first quantitative analysis of size and plumage dimorphism in the family Caprimulgidae. The extent of white markings in the wings, tail and throat of male and female nightjars is scored from museum specimens, and an assessment of plumage dimorphism is provided for each species. Size dimorphism is assessed using data on wing and tail lengths from the literature. Patterns of plumage and size dimorphism in the family are analysed and related to species' ecological attributes, such as the latitude of their breeding ranges and the allocation of parental care between the sexes. The extent of white markings is also related to the structural density of species' preferred breeding habitats, to investigate to what degree the environment may have influenced the evolution of plumage signals. Finally, attempts are made to set the results in a phylogenetic context, using a recent molecular phylogeny of the family.

METHODS

For the purpose of the current study, the Caprimulgidae is defined following the classification of Sibley & Ahlquist (1990), which differs from traditional classifications in assigning the eared-nightjars *Eurostopodus* spp. to their own family, Eurostopodidae. Although this change was not followed in recent monographs on the family (Cleere 1998, Holyoak 2001), evidence from other molecular studies has confirmed the phylogenetically distinct status of *Eurostopodus* (Mariaux & Braun 1996, C. Larsen *in litt.* 2002), and their separation is followed herein. Within the Caprimulgidae, the taxonomy of Sibley & Monroe (1990, 1993) is followed for the classification of genera and species. Three taxa not mentioned therein are added: Bahian Nighthawk *Chordeiles vielliardi* (Lencioni-Neto 1994), Chocó Poorwill *Nyctiphrynus rosenbergi* (Robbins & Ridgely 1992) and Nechisar Nightjar *Caprimulgus solala* (Safford *et al.* 1995). The resulting family hence comprises 82 species in two subfamilies: the Chordeilinae (nighthawks; 10 species) and the Caprimulginae (typical nightjars; 72 species).

White dimorphism

Data on the extent of white markings in the plumage (hereafter 'white') of adult nightjars were obtained from specimens in the bird collection at the Natural History Museum, Tring (NHM). Where possible, five male and five female specimens were inspected for each species. Preference was given to specimens whose label indicated that their sex had been determined using gonad data. For species with distinct races, specimens of the nominate race were measured. In a small number

of cases, it proved necessary to pool individuals of different races, or to measure specimens of a race other than the nominate, to achieve sufficient sample sizes. A few species (particularly Neotropical ones) were not represented in the NHM collection, or were represented by specimens of only one sex. Where this was the case, nightjars were scored for white using any photos or detailed descriptions available in the literature. Three taxa listed by Sibley & Monroe (1990, 1993) and two described more recently are known only from single adult museum specimens, and were excluded from this analysis, as was a sixth species considered extinct (Appendix I).

For each specimen, the number of primaries and rectrices with white markings was noted, and the maximum longitudinal extent of white on each feather was measured parallel to the rachis using dial callipers. The overall length of each feather, from insertion to tip, was measured with a thin, square-ended ruler, and used to convert each absolute measure of white into an integer score between 0 and 10, reflecting the proportion of the feather length showing white markings. For example, a white patch 25 mm in length on a 100-mm long feather would score 3 (20-30% of feather showing white). No attempt was made to quantify the sharpness or contrast of white markings (*cf.* Aragonés *et al.* 1999), and so only areas of pure white plumage were considered: pale markings washed buff or rufous (as shown by several female nightjars) were ignored. Individual feather scores were totalled across the ten primaries and five rectrices to give an overall score of ‘wing white’ (0-100) and ‘tail white’ (0-50) for each specimen. A difference of ≥ 2 between mean male and female scores – i.e. at least 10% of the length of one feather – was taken to define sexual dimorphism in white. Dimorphism was assessed separately for wing and tail markings. For simplicity, species adjudged to show dimorphism in white markings according to these criteria are termed ‘white-dimorphic’.

To provide a single index of overall white, scores of wing and tail white were summed. The difference between male and female scores for overall white was then taken as a measure of ‘absolute’ dimorphism in white markings. However, this index was highly correlated with the overall white score of males (Spearman rank correlation: $r_s = 0.80$, $n = 73$, $P < 0.001$), and was biased in favour of species with extensive white markings. Hence, a second measure (W_{dm}) was also derived, using the equation: $W_{dm} = ((W_m - W_f) / W_m)$, where W_m and W_f represent overall male and female white scores respectively. W_{dm} was independent of male white score ($r_s = 0.20$, $n = 73$, $P > 0.05$), and represented the ‘relative’ dimorphism in white between the sexes, ranging between 0 (sexes similar) and 1 (male with white, female without). Species adjudged to show no significant dimorphism in either wing or tail white (see earlier) scored 0 for W_{dm} , regardless of their absolute scores.

In addition to white markings on the wings and tail, many nightjar species show white patches on the throat. The conspicuousness of these patches can be controlled behaviourally (e.g. Sick 1993), but they are particularly noticeable when birds are vocalising (Cleere 1999, Holyoak 2001). The accurate measurement of throat patches was problematic, not least because their conspicuousness depended greatly on the manner in which the specimen had been prepared. Nevertheless, a coarse index of throat white was obtained using the following categorical scale: 0 = no white; 1 = markings indistinct and/or limited in extent; 2 = one or more conspicuous patches; 3 = extensive white across much of the throat. As with wing and tail markings, only areas of pure white plumage were scored. Scores of throat white were obtained for both sexes of 61 species (Appendix I). No scores were derived for species that were not represented in the NHM collection, and hence could not be inspected directly. Given the imprecise nature of the scoring system, it was considered inappropriate to assess sexual dimorphism in throat white.

Size dimorphism

Morphometric data for male and female nightjars were obtained from the literature. Although body mass is often used for studies of body size dimorphism (e.g. Owens & Hartley 1998), reliable information on mass is frequently difficult to obtain (Rising & Somers 1989), so wing and tail length were used instead. Most data were obtained from Holyoak (2001), the only general reference to provide means and sample sizes for males and females separately. Where the original data were from a single primary source (e.g. Ridgway 1914, Cramp 1985, Fry *et al.* 1988), the latter was consulted directly. For a few species, the data in Holyoak (2001) were very sparse and/or not separated by sex. In these cases, wing and tail measurements obtained from NHM specimens were used instead. A difference of $\geq 10\%$ between mean male and female measurements was used to define dimorphism in wing or tail length (see also Trail 1990). Although some studies use differences of as little as 5% to define sexual dimorphism in linear measures (e.g. Höglund 1989, Owens & Hartley 1998), more conservative criteria were used in the current study, due to the small sample sizes obtained for certain species. Species adjudged to show dimorphism in wing or tail length according to these criteria are termed ‘size-dimorphic’.

Ecological attributes

Data on the breeding habitats of nightjars were gathered from the species accounts in Cleere (1998) and Holyoak (2001). Habitats were graded for structural density (*cf.* Badyaev & Leaf 1997) using the following scale: (1) open grasslands/savannas, steppes and deserts; (2) bushy savannas, heathland, marshes and semi-desert; (3) scrub, open woodland and woodland edges; (4) woodland, plantations, mangroves, scrub forest and forest clearings or edge; (5) forests. A mean habitat score was calculated for each reference source based on the range of habitats listed therein. Mean scores

from the two sources were highly correlated ($r_s = 0.87$, $n = 74$, $P < 0.001$), and an average of these two means was used in all subsequent analyses (Appendix I).

The breeding biology of most nightjars remains poorly documented (Chapter 3), and reliable data on their mating systems are very sparse. Nevertheless, attempts were made to gather data on patterns of parental care, using the species accounts in Cleere (1998) and Holyoak (2001). Any information on the allocation of incubation, brooding and provisioning duties between the sexes was used to assess whether species showed biparental or monoparental care of the offspring. Simple statements regarding monogamy or polygamy were ignored unless supported by further evidence.

Certain studies have suggested that parasite-mediated sexual selection is stronger at lower latitudes (Møller 1998), giving rise to the extravagant sexual ornamentation often noted in tropical species. As a consequence, the potential effect of latitude was also considered in the current study. Latitude was defined as the midpoint of each species' breeding range, according to the distribution maps in Cleere (1998). This method provided a median latitude, and did not take into account the overall extent of breeding ranges (see Cardillo 2002), but was sufficient for the purposes of the current study. Where species had distinct races, latitude was taken for the range of the race scored for white.

Phylogenetic control

Comparative studies using species-level data are potentially confounded by the varying degree of common phylogenetic ancestry among species (Bennett & Owens 2002). Closely related species can not be considered statistically independent, and may share characters due to common descent rather than independent evolution (see Harvey & Pagel 1991). Most contemporary comparative studies attempt to control for the effects of phylogeny by identifying independent evolutionary events, often using the independent comparisons method first outlined by Felsenstein (1985). The latter is based on the principle that evolutionary change in a trait among species radiating from a single node is independent of the evolution of traits elsewhere in the phylogeny. In the current study, the Comparative Analysis by Independent Contrasts (CAIC) program was used to identify and calculate independent 'contrasts' from the data set (Purvis & Rambaut 1995).

The power of the independent comparisons method depends on the detail and accuracy of the phylogeny used (Promislow *et al.* 1992). Although there have been a number of studies of higher level relationships within the Caprimulgiformes (Cracraft 1981, Sibley & Ahlquist 1990, Mariaux & Braun 1996, Mayr 2002), generic and specific relationships in the Caprimulgidae remain poorly understood. To date, the only published data on phylogenetic relationships within the family are

those provided for 11 caprimulgid species in Sibley & Ahlquist (1990). However, a molecular phylogeny of the Caprimulgidae, based on cytochrome *b* sequence analysis, is currently being developed (C. Larsen *in litt.* 2002), and a draft of this tree was made available for the current study. Only 17 of the 82 species recognised by the current study were represented in this phylogeny (Figure 5.1) but, where there were species in common, the proposed relationships were in agreement with Sibley & Ahlquist (1990). The latter noted the considerable genetic diversity hidden by conserved external appearance within the family, and both phylogenies highlight the need for the generic status of many taxa to be revised. Nevertheless, where appropriate, this framework was incorporated into the following analyses to set the results in a phylogenetic context.

Statistical analysis

All continuous data were tested for normality and homoscedasticity prior to analysis. Data for male and female white scores showed bimodal distributions and resisted all attempts at normalisation, so non-parametric tests were used in most analyses. Statistical significance was set at $P < 0.05$ in all cases. Means are given \pm one standard error. Categorical data were analysed using the *G*-test of independence.

Felsenstein's (1985) independent comparisons method, as applied by CAIC, makes a number of evolutionary and statistical assumptions (see Purvis & Rambaut 1995), several of which were not met by the data in the current study. Although use of the CRUNCH algorithm of CAIC is typically recommended for continuous data, the BRUNCH algorithm was used in the current study, as it makes fewer assumptions about the evolutionary model fitted to the data. BRUNCH produces fewer contrasts than CRUNCH, as it does so only where an evolutionary change occurs in the independent variable (rather than at all bifurcating nodes). It also proved necessary to use non-parametric (rather than regression) methods when analysing these contrasts, as diagnostic tests revealed that a number of statistical assumptions were violated by the data. As a consequence, most tests of significance following phylogenetic control were highly conservative.

RESULTS

White dimorphism

In total, 521 specimens of 66 species were measured and scored for wing and tail white, and sufficient information was obtained from the literature to derive white scores for a further seven species. Too little information was available to score the female plumage of two species, which were hence excluded from dimorphism analyses. One further species, Egyptian Nightjar *Caprimulgus aegyptius*, was excluded because of difficulties defining the extent of the white markings in its wing. Thus, white scores were obtained for both sexes of 73 (89%) of the 82 species of nightjar recognised by the study (Appendix I).

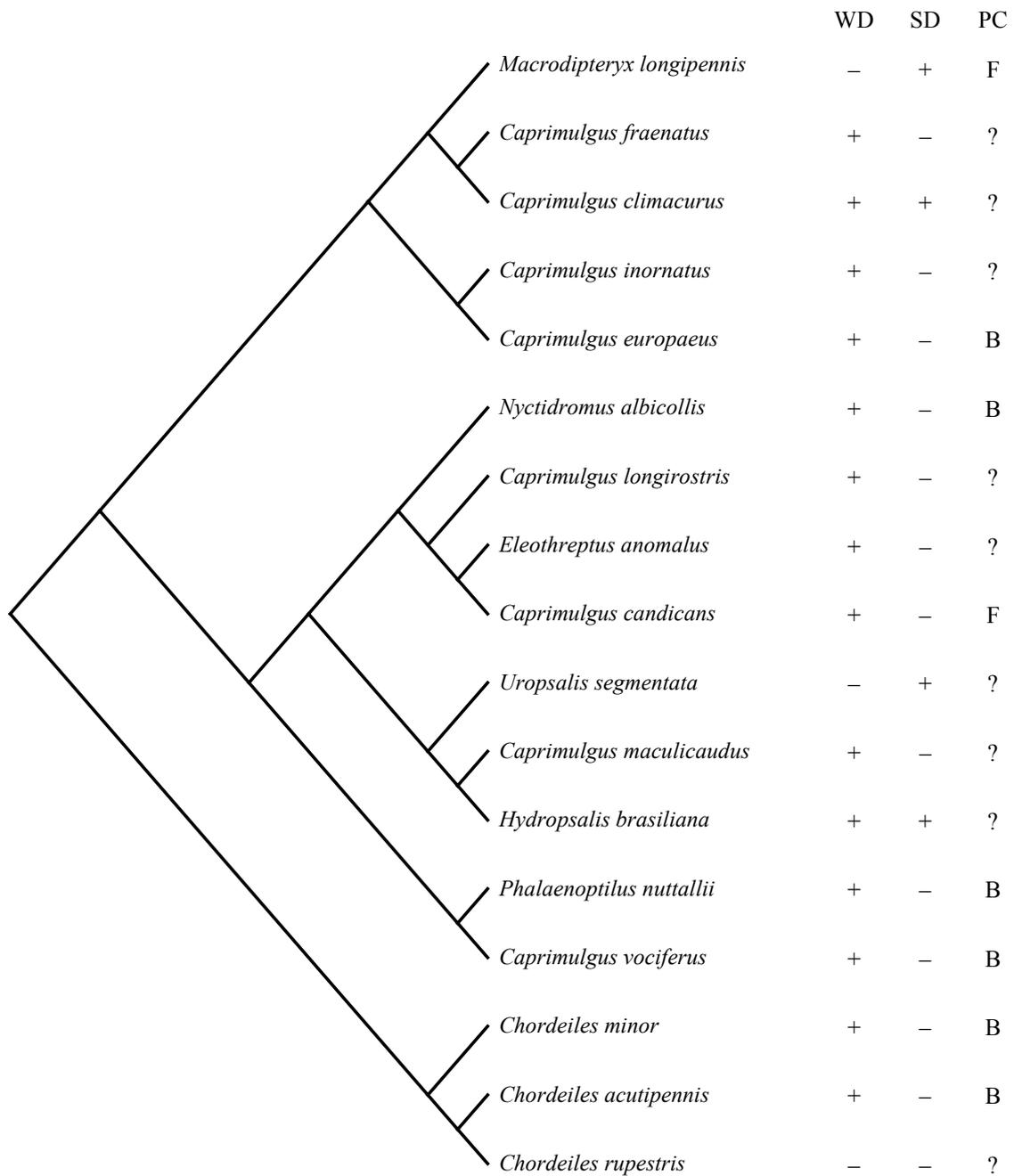


Figure 5.1 Phylogenetic hypothesis for the relationships of 17 species of Caprimulgidae, based on analysis of cytochrome *b* sequence data (C. Larsen *in litt.* 2002). The occurrence (+) or absence (-) of white dimorphism (WD) and size dimorphism (SD) is indicated for each species, based on the results of the current study. The allocation of parental care (PC) between the sexes is also given (from Cleere 1998, Holyoak 2001): ‘B’ = both sexes care; ‘F’ = female only cares; ‘?’ = uncertain.

Across all species, there was a significant positive correlation between wing and tail white for male ($r_s = 0.34$, $n = 73$, $P = 0.003$) and female ($r_s = 0.30$, $n = 73$, $P = 0.009$) nightjars. Figure 5.2a reveals one conspicuous outlier, the male Pennant-winged Nightjar *Macrodipteryx vexillarius*, which shows extensive white markings in the wings but none in the tail. Within the subset of species for which scores of throat white were obtained, there was a positive correlation between throat and overall white scores for males ($r_s = 0.29$, $n = 64$, $P = 0.019$) and females ($r_s = 0.50$, $n = 64$, $P < 0.001$). The male White-winged Nightjar *Caprimulgus candicans* was the notable exception, with extensive white in the wings and tail, but none on the throat (Figure 5.2b). When phylogenetic control was introduced, none of the above correlations remained significant (all $r_s < |0.50|$, $n = 5$ to 8 , $P > 0.05$).

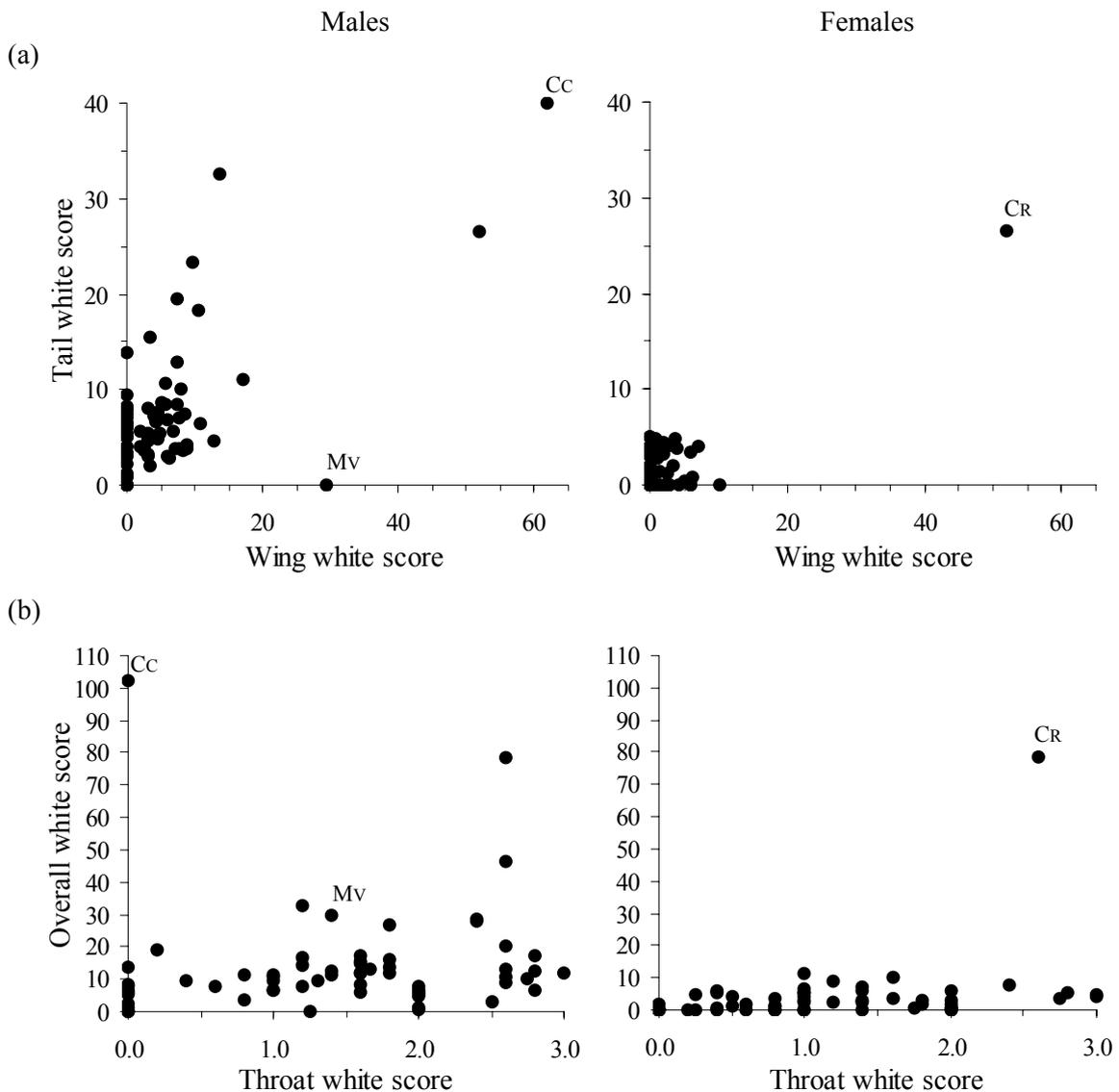


Figure 5.2 White scores for wings, tail and throat of male and female nightjars: (a) wing versus tail white; (b) throat versus overall white. Labeled are *Caprimulgus candicans* (CC), *Chordeiles rupestris* (CR), and *Macrodipteryx vexillarius* (MV).

The males of just four species lacked any white in the wings and tail, with the majority (89%) showing white scores in the range 0.5-30 (Figure 5.3a). Four species scored over 30, most notably the White-winged Nightjar, with a score of 102. When considering females, 28 (38%) species lacked white wing and tail markings entirely, and all but one scored less than 12 for overall white (Figure 5.3b). The exception was the monomorphic Sand-coloured Nighthawk *Chordeiles rupestris*, which scored 78.5. Fifty-eight (79%) species showed some sexual dimorphism in overall white, but the White-winged Nightjar was by far the most extreme in absolute terms (Figure 5.3c). On average, males of white-dimorphic species had higher white scores than monomorphic species (14.2 ± 1.9 versus 8.2 ± 5.1 ; Mann-Whitney *U*-test: $W = 240$, $n_1 = 58$, $n_2 = 15$, $P < 0.001$), whereas there was no significant difference for females (2.3 ± 0.4 versus 8.0 ± 5.1 ; $W = 636$, $n_1 = 58$, $n_2 = 15$, $P > 0.05$). The mean for females of monomorphic species was considerably inflated by the aberrant Sand-coloured Nighthawk: when this species was excluded, the mean was 2.9 ± 0.7 ($n = 14$). CAIC identified just three contrasts when phylogenetic control was introduced.

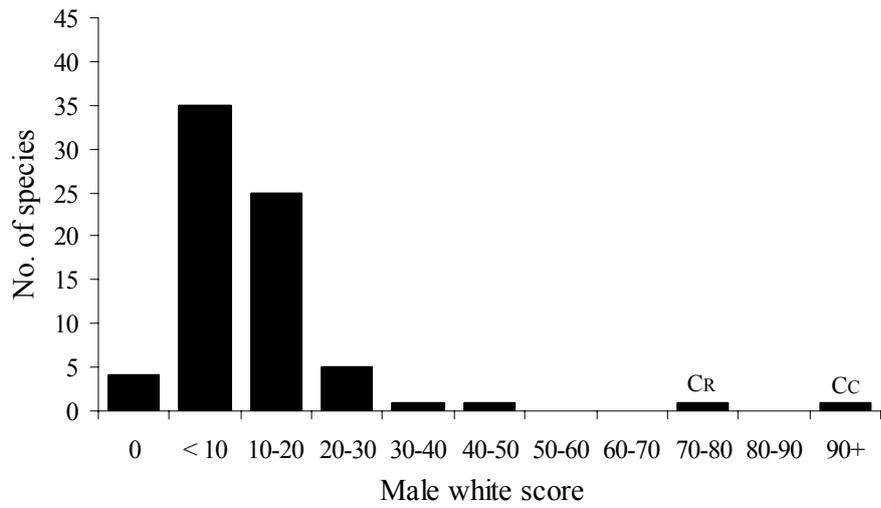
Most (35 of 58) white-dimorphic species showed sexual dimorphism for both wing and tail scores. However, 22 species were dimorphic for tail white only, and one species (Pennant-winged Nightjar; see earlier) was dimorphic only for wing white. Overall, 36 (49%) species showed sexual dimorphism in wing markings. The males of these species scored significantly higher than monomorphic species for wing white (8.9 ± 1.7 versus 2.5 ± 1.4 ; $W = 825$, $n_1 = 36$, $n_2 = 37$, $P < 0.001$); there was no such difference in female scores (1.8 ± 0.4 versus 2.3 ± 1.4). Almost 75% (27 of 37) of monomorphic species lacked any white in the wing.

Sexual dimorphism in tail white was shown by 57 (78%) species. Dimorphism was significantly more common for tail markings than wing markings (*G*-test: $G = 13.19$, $df = 1$, $P < 0.001$). In only five species did males entirely lack white tail markings. Males of species that were dimorphic for tail markings had significantly whiter tails than monomorphic species (8.3 ± 0.9 versus 3.8 ± 1.6 ; $W = 288$, $n_1 = 57$, $n_2 = 16$, $P < 0.001$). The reverse was apparently true in females: those of dimorphic species scored significantly less for tail white than monomorphic species (0.9 ± 0.2 versus 3.7 ± 1.6 ; $W = 764$, $n_1 = 57$, $n_2 = 16$, $P = 0.013$).

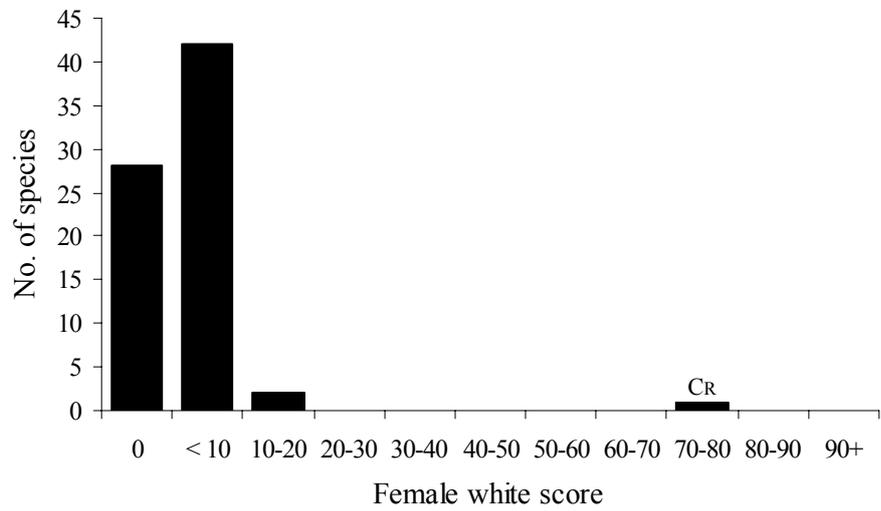
Size dimorphism

Data for wing and tail length were obtained for 75 species of nightjar (Appendix I). No mean data were available for females of one species, but the ranges provided elsewhere gave no obvious indication of size dimorphism. Following the criteria of the study, ten species showed sexual dimorphism in wing or tail length (or both): in all cases, the male was the larger sex. In two species of the Afrotropical genus *Macrodipteryx*, size dimorphism took the form of elaborate structural ornaments in the inner primaries, manifest only in the breeding plumage of the definitive male.

(a)



(b)



(c)

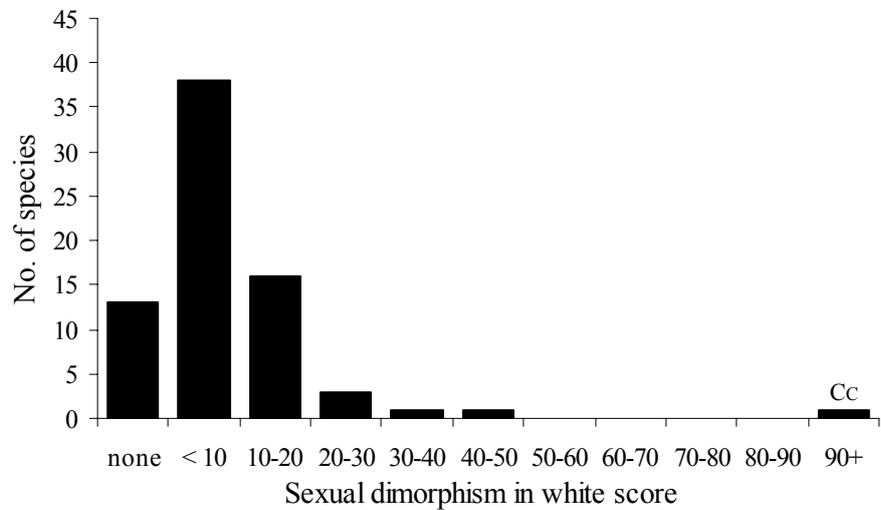


Figure 5.3 Overall white scores and absolute dimorphism in white for males and females of 73 species of nightjar. Labeled are *Caprimulgus candicans* (CC) and *Chordeiles rupestris* (CR).

Four species displayed sexual dimorphism in tail length of 10-40%; the remaining four species (all Neotropical) showed more extravagant tail ornamentation.

When considering all 73 species for which both sets of data were available, there was no significant association between the occurrence of size and white dimorphism ($G = 0.54$, $df = 1$, $P > 0.05$). Similarly, there was no significant difference in overall white scores for males of size-dimorphic or monomorphic species (14.9 ± 5.2 versus 12.7 ± 2.0 ; $W = 2330$, $n_1 = 10$, $n_2 = 63$, $P > 0.05$). However, there was a non-significant trend for females of size-dimorphic species to score less for overall white than their monomorphic counterparts (1.0 ± 0.6 versus 3.9 ± 1.3 ; $W = 2445$, $n_1 = 10$, $n_2 = 63$, $P = 0.061$).

Ecological attributes

Investigation of the potential effect of habitat structure on white markings revealed a significant negative correlation between habitat density and overall white score for male ($r_s = -0.42$, $n = 73$, $P < 0.001$) and female nightjars ($r_s = -0.30$, $n = 73$, $P = 0.011$; Figure 5.4a). When wing and tail scores were considered separately, it became apparent that this relationship was the result of a strong negative correlation between habitat density and wing white (males: $r_s = -0.53$, $n = 73$, $P < 0.001$; females: $r_s = -0.49$, $n = 73$, $P < 0.001$; Figure 5.4b). There was no significant relationship, meanwhile, between habitat density and tail white (both sexes: $r_s < |0.20|$, $n = 73$, $P > 0.05$; Figure 5.4c) or throat white (both sexes: $r_s < |0.20|$, $n = 64$, $P > 0.05$). CAIC identified eight contrasts where habitat density increased, but for none of the four significant relationships above did changes in white score differ significantly from zero (Wilcoxon signed ranks test: all $T < 10$, $n = 8$, $P > 0.05$).

When considering plumage dimorphism, no significant correlation was found between habitat density and either measure of white dimorphism used in this study (absolute: $r_s = -0.22$, $n = 73$, $P > 0.05$; relative: $r_s = 0.04$, $n = 73$, $P > 0.05$). Similarly, there was no significant relationship between habitat density and size dimorphism, with nearly identical scores of habitat density for size-dimorphic and monomorphic species (3.1 ± 0.2 versus 3.1 ± 0.1 ; $W = 2326$, $n_1 = 10$, $n_2 = 63$, $P > 0.05$).

For most species, the information provided in the literature was too limited to draw firm conclusions regarding the allocation of parental care between the sexes. Nevertheless, unequivocal evidence of biparental care was obtained for 28 species in the current study (Appendix I). None of these species showed sexual size dimorphism, in contrast to 10 of 47 species for which the nature of parental care was not known. Hence, the data suggested that confirmed biparental carers were less likely to show size dimorphism ($G = 9.71$, $df = 1$, $P < 0.005$). In contrast, the frequency of

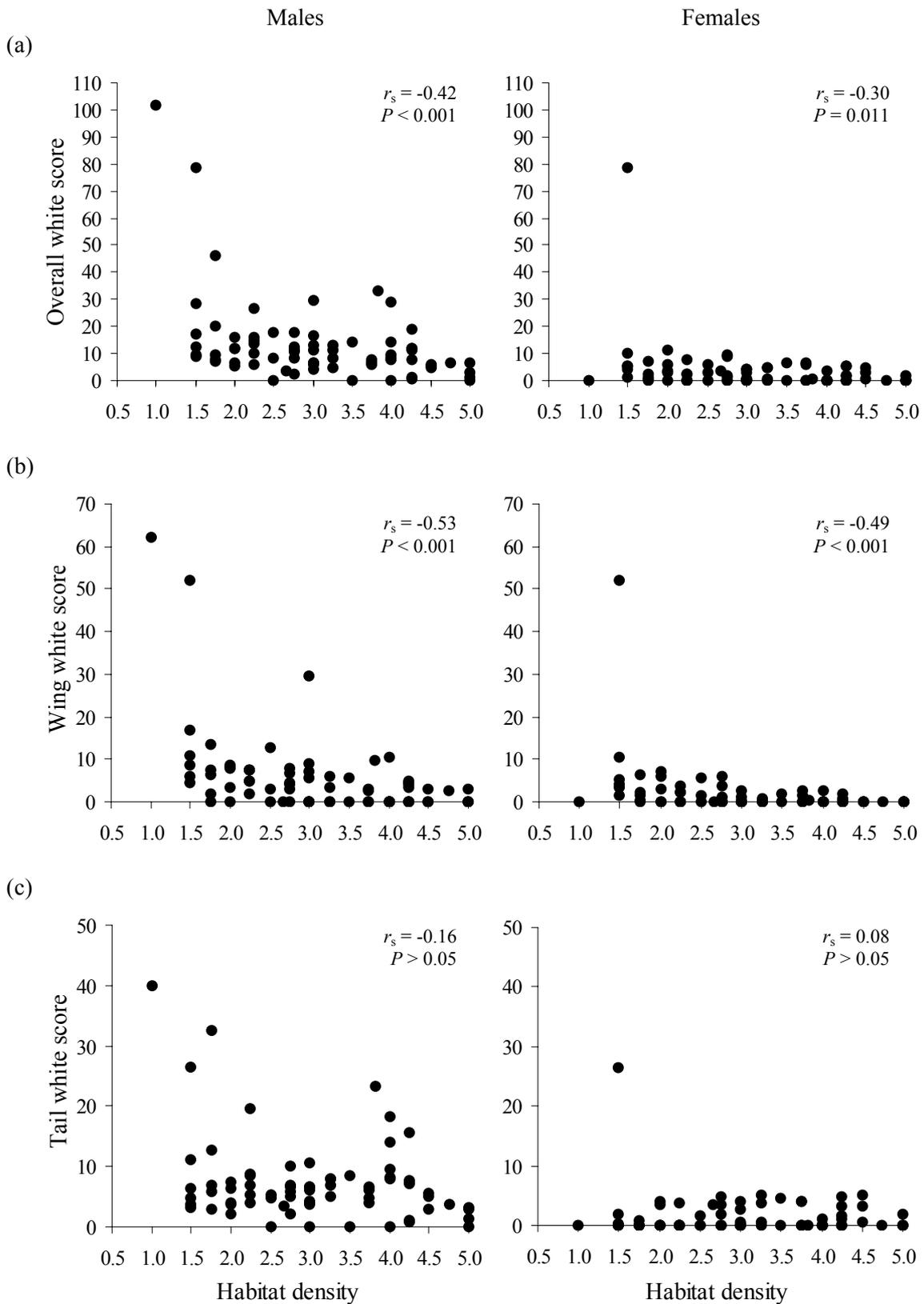


Figure 5.4 Relationship between wing and tail white scores of 73 nightjar species and the structural density of their preferred breeding habitats. Lower values for habitat density indicate more open habitats (see Methods).

white dimorphism (assessed as a categorical variable) among confirmed biparental carers did not differ significantly from that observed among the remaining, unclassified, species (3 of 26 *versus* 12 of 47; $G = 2.07$, $df = 1$, $P > 0.05$).

Across all species, no relationship was found between median latitude of breeding range and extent of white dimorphism, regardless of whether the latter was treated as an absolute ($r_s = 0.22$, $n = 73$, $P > 0.05$) or relative measure ($r_s = 0.04$, $n = 73$, $P > 0.05$). However, if plumage dimorphism was treated as a categorical variable, white-dimorphic species bred at higher latitudes than their monomorphic counterparts ($16.2 \pm 1.6^\circ$ *versus* $8.3 \pm 1.9^\circ$; unpaired t -test: $t_{71} = 2.40$, $P = 0.019$). There was no such significant difference in breeding latitude for species that were dimorphic or monomorphic for size ($8.6 \pm 2.3^\circ$ *versus* $15.5 \pm 1.5^\circ$; $t_{71} = -1.77$, $P = 0.082$).

DISCUSSION

This chapter represents the first comprehensive study of size and plumage dimorphism in the family Caprimulgidae. Relatively few studies have investigated variation in nightjar white markings in a quantitative manner (Ingels & Ribot 1982, Forero *et al.* 1995, Aragonés *et al.* 1999), and this is the first attempt to do so for the majority of species in the family. Unfortunately, the delicacy and, for many species, limited number of museum specimens meant that the precise measurement of white, and a statistical assessment of dimorphism, was not possible (*cf.* Forero *et al.* 1995). Nonetheless, the scoring system and definition of dimorphism used in the current study provided a relatively precise assessment of white extent and dimorphism, which compared well with the qualitative information available in the literature (e.g. Cleere 1998, Holyoak 2001).

Overall, considerable variation in the extent of white markings was apparent across the species of the family, most notably among males. The males of just four species lacked white in the plumage of the wings and tail, whereas the whitest male was that of the White-winged Nightjar *Caprimulgus candicans*. In contrast, 40% of female nightjars showed no white in the wings and tail, with all but one species scoring less than 12 overall. The exception was the monomorphic Sand-coloured Nighthawk *Chordeiles rupestris*, a diurnal species of the sandbars and river beaches of Amazonia. The bold wing and tail markings of this species have been noted by a number of authors (e.g. Sick 1993, Aragonés *et al.* 1999), and are almost certainly linked to its gregarious habits and the benefits of prominent 'flash marks' in a flocking species (see Brooke 1998).

Almost 80% of nightjar species assessed were adjudged to show some sexual dimorphism in wing or tail white. In practice, the true proportion of dimorphic species may be slightly higher, with more subtle cases of dimorphism overlooked by the slightly conservative criteria employed. The Red-necked Nightjar *Caprimulgus ruficollis*, for example, was adjudged not to show

dimorphism in wing white in the current study (male and female scores differed by 1.6), whereas significant sexual differences in wing patch size were found in a study of *c.* 40 adult birds (Forero *et al.* 1995). Broadly, however, the proportion of white-dimorphic species coincided well with the 80-90% given for the family in a more general study of plumage dichromatism in birds (Bennett & Owens 2002). Although the male was consistently the whiter or ‘more colourful’ sex – as predicted by Butcher & Rohwer’s (1989) ‘first rule of avian colour dimorphism’ – the data for two species suggested slight female-biased dimorphism (Rufous-bellied Nighthawk *Lurocalis rufiventris* and Collared Nightjar *Caprimulgus enarratus*). In neither species, however, were the differences significant according to the criteria of the current study, nor was any corroboratory evidence subsequently found in the literature.

The results of this study suggested that sexual dimorphism was significantly more common in tail markings than in wing markings. Observations from better known species suggest that nightjar wing and tail patches are used primarily as intra-specific signals, directed at potential competitors or prospective mates (Mengel 1972, Bruce 1973, Cramp 1985, Clay *et al.* 2000; Chapter 3). However, whilst wing markings can be exposed very effectively during display flights or when hovering, tail markings are potentially useful in a wider range of habitats and situations. Furthermore, since tail markings typically occur on the tips and/or outer edges of tail feathers, they are less easily concealed at rest than wing markings. Hence, while sexual selection may favour more conspicuous tail markings in males, predation pressures could select for reduced tail white in females (Martin & Badyaev 1996) – the sex responsible for the greater share of parental duties at the nest in many species – leading to sexual differences in their extent. Support for this proposal was provided by the observation that males had significantly whiter, and females significantly less white, tails in species dimorphic for tail white than in their monomorphic counterparts.

The influence of the environment on the extent of plumage markings was illustrated by the analysis of species’ white scores *versus* the structural density of their breeding habitats. A negative relationship was apparent for both male and female nightjars, with extent of wing and tail white decreasing significantly as habitat density increased. This result was in marked contrast to the findings of a study of plumage markings in *Phylloscopus* warblers, where species of darker habitats were shown to have more, and brighter, pale patches than species of more open habitats (Marchetti 1993). In nightjars, the relationship between habitat and overall white score was the result of a strong negative correlation between habitat density and wing white; no such relationship existed with tail white. As noted earlier, wing markings are most effectively exposed during flight, and hence may not serve as very efficient long-range signals in dense habitats, where visibility and the possibilities for flight are much reduced. Species of denser habitats tend to rely more on vocal signals, and tail and throat markings, which can be exposed for communication over shorter

distances. The pale markings of *Phylloscopus* warblers, meanwhile, are usually visible under normal circumstances, but play an important role during close-range agonistic displays between males at territorial boundaries (Marchetti 1993).

In contrast to the high proportion of plumage-dimorphic species, less than 14% of species assessed showed clear evidence of sexual size dimorphism. However, the morphometric data available and somewhat conservative criteria used, meant that, in practice, this was less an assessment of overall body size dimorphism, and more an indication of wing and tail ornamentation. Although in all ten dimorphic species identified the male was the larger sex, the tail of the male Sickle-winged Nightjar *Eleothreptus anomalus* was apparently *c.* 9% shorter than the female, and hence only narrowly failed to meet the definition of dimorphism used herein. Interestingly, data from a larger sample of birds indicated that adult male Sickle-winged Nightjars do indeed have significantly shorter tails than females (74.8 mm *versus* 84.6 mm, $t = 8.80$, $n = 69$, $P < 0.05$; D. Buzzetti *in litt.* 2002).

The lack of any significant association between plumage and size dimorphism supported suggestions that these two types of dimorphism correlate with different aspects of social and reproductive behaviour (Owens & Hartley 1998). Unfortunately, the dearth of data on the breeding biology of many nightjar species (Chapter 3) meant that it was not possible to investigate covariation of dimorphism with social mating system or levels of extra-pair paternity. Better information was available on the allocation of parental duties between the sexes, but the classification of parental care was still somewhat problematic, not least because of the difficulties associated with establishing monoparental care (see Chapter 3). Nevertheless, it was noteworthy that confirmed biparental carers (i.e. socially monogamous species) were significantly less likely to show size dimorphism than other, unclassified species. Size dimorphism is typically associated with polygamy and high levels of intra-sexual competition (e.g. Payne 1984, Höglund 1989, Andersson 1994, Owens & Hartley 1998, Székely *et al.* 2000), and is hence unexpected in biparental carers. Female-only care has so far been proven for only three nightjar species: two species of the Afrotropical genus *Macrodipteryx* (Fry *et al.* 1988, Holyoak 2001) and the White-winged Nightjar (this study). Although the two *Macrodipteryx* species both show conspicuous sexual dimorphism of their extravagant wing ornament, the White-winged Nightjar was monomorphic for size (see also Chapter 2).

All of the findings discussed above are the result of analyses conducted using species-level data, and are hence potentially confounded by differing levels of phylogenetic relatedness among species (e.g. Harvey & Pagel 1991, Bennett & Owens 2002). Although attempts were made to control for the effects of phylogeny, using a recent molecular study of relationships within the family, just 17

of the 82 species recognised by the current study were represented in this phylogeny. As a result, the number of evolutionary independent contrasts identified by CAIC was consistently very low, and tests of significance following phylogenetic control were very limited in power (where they were possible at all). Consequently, conclusions regarding the phylogenetic validity of the raw analyses are clearly somewhat limited. However, the most parsimonious interpretation of the findings (in the context of the phylogenetic information available) would suggest that the ancestral caprimulgid was socially monogamous, sexually dimorphic for plumage, and monomorphic for size (Figure 5.1). The evidence also suggests that any subsequent changes from this ancestral state may have occurred in conjunction with changes in mating system and, in one case, the evolution of flocking behaviour.

CONCLUSIONS

This chapter has provided an overview of patterns of sexual size and plumage dimorphism in the Caprimulgidae, and has attempted to set the White-winged Nightjar in the context of its family as a whole. The study species has been shown to be a highly unusual member of the family, most notably in the spectacular extent of the white in the wings and tail (but not throat) of the male. Although a relationship between white markings and habitat openness was demonstrated for the family, this could not explain the extreme plumage dimorphism shown by the White-winged Nightjar. Furthermore, unlike the two other species for which polygyny and female-only parental care have been demonstrated, the White-winged Nightjar is monomorphic in size (see also Chapter 2). The reasons why the study species should be such an atypical representative of its family are discussed further in Chapter 6.

CHAPTER 6

CONCLUSIONS

When this thesis was first conceived, the White-winged Nightjar was considered one of the most threatened and poorly known birds in the Neotropics (Chapter 1). The species was known from just three sites in Brazil, Bolivia and Paraguay, and despite its ‘Critical’ status (Collar *et al.* 1994) and high research priority (Parker *et al.* 1996), its basic ecology and conservation requirements remained very poorly understood. This three-year study was undertaken with the aim of generating some of the information needed to clarify the species’ status and facilitate future conservation efforts on its behalf. Furthermore, as a striking and enigmatic species of South America’s cerrado habitats, it was hoped that this study would help to raise awareness of grassland bird conservation in general, and also stimulate further investigation into the management of Paraguay’s protected cerrado sites.

As outlined in Chapter 1, the success of species-based conservation efforts depends on the correct diagnosis, and appropriate treatment, of the causes of rarity or population decline (e.g. Caughley 1994, Caughley & Gunn 1996, Green 2002). This process requires a sound knowledge of a species’ natural history and ecology, without which mistakes can be made when diagnosing potential agents of decline. In the case of the Seychelles Magpie-robin *Copsychus sechellarum*, for example, it took an ecological study of the species’ distribution and behaviour to highlight the influence of habitat change in limiting population recovery following the eradication of introduced predators (Caughley & Gunn 1996). Ecological and behavioural studies have a central role to play in solving many conservation problems, with important contributions to make in a variety of areas (see Caro 1998, Sutherland 1998). The breeding system of a species, for instance, can have a profound influence on a number of issues pertinent to conservation, including effective population size, reproductive skew, genetic diversity and inbreeding depression (Caughley 1994). Moreover, a good understanding of a species’ ranging behaviour, habitat requirements and diet is essential for the diagnosis of current and future threats, the identification and design of new protected areas, and the effective implementation of management policies in existing reserves (Green 2002). Surveys and population estimates, meanwhile, require the use of census techniques that reflect a species’ movement patterns, detectability, and communicatory behaviour (Bibby *et al.* 2000, Underhill & Gibbons 2002). Furthermore, in certain cases, the behaviour of a species itself may prove worthy of conservation, and can serve to promote popular interest in the natural world and conservation issues (Dingle *et al.* 1997, Sutherland 1998).

KEY FINDINGS

First-year White-winged Nightjars of both sexes exhibited a pre-definitive plumage similar to that of the definitive female. Young females bred when approximately 12 months old, and attained definitive plumage at the end of their first breeding season. Young males meanwhile displayed a form of delayed plumage maturation, spending the majority of their first potential breeding season in a conspicuously intermediate state of moult (Chapter 2). Although first-year males were regularly seen in the vicinity of display territories, they did not appear to establish their own arenas, and no evidence was obtained to suggest that they succeeded in breeding (Chapter 3). Despite the extreme sexual plumage dimorphism shown by the species, adult White-winged Nightjars were monomorphic for all size measures investigated, except wing curvature (Chapter 2). The curved outer primaries of definitive males were apparently involved in the production of dull mechanical noises during display flights. Since primary moult proceeded descendantly in the study species, first-year males did not acquire these curved primaries until late in their first potential breeding season, and produced only weak and high-pitched display noises in the interim (Chapter 3).

Male display activity commenced in late August and continued through until early January. Display rate was highest when males first arrived at display arenas at dusk, but, after an initial burst, activity levels were best predicted by ambient levels of moonlight. Although there was no evidence for consistent inter-male differences in display rate, males did show individual variation in the temporal measures of the “tk... grrrrr” display noise. Female nightjars carried out all incubation, brooding and provisioning duties, apparently only visiting display arenas to copulate. Females made two nesting attempts per breeding season, each initiated within two days of a full moon (Chapter 3). Although nest sites were in the normal home range of females, there was no compelling evidence to suggest that they fell within the boundaries of nearby male display territories (Chapter 4). Chick paternity analyses indicated that the nearest territory-holding male was not necessarily the father of a brood (Chapter 3). Males showed very restricted ranging behaviour during the breeding season, when they were rarely located further than 150 m from their display arenas (Chapter 4). Arenas were aggregated in areas of open campo cerrado vegetation on the upper slopes of ridgelines (Chapter 3), and potentially at traditional sites, which were rather peripheral to the male non-breeding ranges in some cases (Chapter 4).

As also suggested by patterns of flight-feather moult (Chapter 2), radio-tagged nightjars showed no evidence of migratory behaviour, remaining faithful to the same area throughout the eight to ten months for which they were monitored (Chapter 4). Home ranges were 20 to 40 ha in size, and contained a disproportionately large amount of young campo cerrado vegetation, but no forest or old campo cerrado habitats. Within home ranges, nightjars preferred younger and avoided older campo cerrado vegetation when foraging, potentially due to the greater abundance and accessibility

of insect prey in the former. Nevertheless, radio-tagged nightjars did avoid the most recently burnt habitats, suggesting that there was some delay before birds recolonised areas following fires. When selecting their daytime roosts, nightjars avoided the youngest and oldest habitats, with the vegetation characteristics of roost sites suggestive of a trade-off between cover and access (Chapter 4). Observations of nightjars inactive at roost sites on cold nights during the non-breeding season hinted that birds may occasionally enter torpor (Chapter 4).

Although almost 80% of caprimulgid species exhibit some sexual dimorphism in wing or tail white, the White-winged Nightjar was shown to be by far the most extreme case, in terms of both male whiteness and overall dimorphism (Chapter 5). The extent of white in the male plumage was at least partly predicted by a family-wide relationship between wing white and structural openness of breeding habitats (Chapter 5), but this failed to explain the complete absence of white in the female, or indeed the extent of the plumage dimorphism shown by the species overall. The most parsimonious interpretation of the evidence, in the context of the phylogenetic information available, suggested that extreme plumage dimorphism has evolved in the White-winged Nightjar in conjunction with a polygynous mating system and female-only care (Figure 5.1). This was in contrast with the two other species for which polygyny has been proven, which both show sexual dimorphism in structural plumage ornaments.

THE WHITE-WINGED NIGHTJAR: A VERY ATYPICAL CAPRIMULGID

By far the most striking feature of the White-winged Nightjar is the conspicuous white plumage of the male, which was so extreme as to cause early naturalists to speculate that the type specimen might be an albino variety (Pelzeln *in* Sclater 1866). At rest, this white plumage is surprisingly well concealed, with the location of conspicuous markings closely fitting the model predicted by the ‘restricted signalling strategy’ (Aragonés *et al.* 1999). In flight, however, the male is unmistakable, with only the Sand-coloured Nighthawk *Chordeiles rupestris* coming close in terms of extent of white in the wings and tail (Chapter 5). The nighthawk is a diurnal species of open fluvial habitats (Sick 1993), and almost certainly evolved its bold wing and tail markings in conjunction with its flocking habits (see Brooke 1998). The case of the study species, however, is more puzzling: why exactly is the male White-winged Nightjar so white? I suggest that the answer to this lies in a combination of the species’ mating system and open-country habits.

This study demonstrated that the study population of White-winged Nightjars practises a polygynous, possibly lekking or ‘landmark’, mating system (Chapter 3). Although the breeding biology of most nightjars remains poorly known, male emancipation from parental care is apparently relatively uncommon in the Caprimulgidae, with polygyny only demonstrated convincingly for two other species: the Standard-winged Nightjar *Macrodipteryx longipennis* and

Pennant-winged Nightjar *M. vexillarius* (Fry *et al.* 1988, Holyoak 2001). The White-winged and Standard-winged Nightjars are both species of savanna habitats, and potentially profit from the mass hatches of winged termites and ants that occur during the summer rains (Jackson 2000a,b; Chapter 3). Although abundant, this potential food source is both sporadic and patchy, and would probably necessitate females having large home ranges, which males could not defend economically (Emlen & Oring 1977). As a consequence, males might most profitably congregate on landmarks or leks, as observed in species of grouse (Bradbury *et al.* 1986) and antelope (Clutton-Brock 1989) where the females show large home ranges.

Once started down the path of a lekking or landmark system, it can be seen more easily how the extreme plumage dimorphism of the study species might evolve. Male nightjars aggregate on the upper slopes of ridgelines, where the relief and open vegetation favour long-range visibility, and display to attract passing females (Chapter 3). As a specialist of open-country habitats, male White-winged Nightjars fully exploit the potential for visual signalling, and evolve extensive white plumage and an acrobatic flight display to further increase their conspicuousness, particularly under moonlit conditions (Chapter 3). Females, meanwhile, conduct all of the incubation, brooding and provisioning of the offspring alone, and are strongly influenced by selection pressures linked to nest predation, which favour increased crypsis (e.g. Martin & Badyaev 1996). Furthermore, as their interaction with males involves little more than soliciting copulations at display arenas, females have little need for the plumage markings displayed by certain socially monogamous species during intra-pair interactions (e.g. Vilella 1995). The net result is the situation we see today: the extreme white plumage of the male, and the drab plumage of the female, lacking even the limited white (or buff) markings shown by females of many other open-country species (Figure 5.4).

Unfortunately, the limited data obtained on chick paternity, and the difficulties involved in observing and documenting interactions at display arenas, meant that it did not prove feasible to estimate male reproductive success, or investigate its potential correlates. Male display activity was influenced primarily by climatic conditions, the effects of which masked any potential inter-male variation in display rate (Chapter 3). Furthermore, although inter-male differences in plumage whiteness were documented during this study, attempts to relate them to male age proved inconclusive (Chapter 2). Nevertheless, it was of considerable interest to note that first-year males manifest an unusual form of delayed plumage maturation, whereby they spent their first potential breeding season in an intermediate state of moult between the (female-like) pre-definitive plumage and the definitive white plumage.

Delayed plumage maturation is not well documented in the Caprimulgidae, although it is known to occur in males of the two species from the genus *Macrodipteryx* (Stresemann & Stresemann 1966).

Numerous models have been proposed to explain its adaptive significance (see Thompson 1991), but the central tenet of most is that young males will have very low expected reproductive success if they attempt to breed during their first season. This scenario is perfectly feasible in polygynous species, such as the White-winged Nightjar, where there is considerable competition among males for females and/or display sites. However, the conspicuous intermediate plumage shown by first-year males of the study species did not fit well with either the ‘female-mimicry’ (males mimic females to gain access to adult male territories) or ‘crypsis’ (males sport cryptic plumage to reduce predation risk) hypotheses. Instead, the best explanation is apparently provided by the ‘status signalling’ hypothesis of Lyon & Montgomerie (1986), which suggests that, in systems where females prefer bright males, dull plumage serves as a reliable signal of subordinate status, and reduces the amount of aggression experienced by young males from adult males. This hypothesis was lent support by observations during this study that suggested that definitive males often tolerated the presence of first-year males near their display arenas, despite frequent aggressive interactions between territory-holding males (Chapter 3).

CONSERVATION IMPLICATIONS AND RECOMMENDATIONS

The results of this study have numerous important implications for the conservation of the White-winged Nightjar and the management of its habitats. The sex bias observed in the adult captures (Chapter 2) seems likely to have been an artefact of the greater conspicuousness of males (particularly during the breeding season), rather than a true reflection of any skew in population sex ratio. Nevertheless, the finding that the study population practises a polygynous, possibly even lekking, mating system has potential consequences for reproductive skew and effective population size (Sutherland 1998). Furthermore, if male display territories are located at traditional sites, these areas could be of special importance to the population, with limited possibilities for relocation if they are destroyed (Clay *et al.* 2000). As with most species of grassland bird at the study site, the White-winged Nightjar was found to nest between September and December, on the ground amongst wet grassland or campo cerrado vegetation (Chapter 3). Any wildfires during the nesting period could have a disastrous effect on breeding success (see also Capper *et al.* 2000), and extensive burns in the latter half of August could also disrupt nesting if vegetation did not regrow sufficiently before the onset of breeding activity.

The influence of fire on vegetation structure was also a central theme running through the findings of studies of habitat selection by roosting and foraging nightjars (Chapter 4). Nightjars roosted in campo cerrado and (less frequently) wet grassland habitats, apparently selecting sites that provided protection from the elements and potential predators, and easy access, often in the form of a small clearing or ‘runway’ adjacent to the roost site. This simultaneous need for cover and access probably explained why roosting birds tended to avoid the youngest (too little vegetation cover)

and oldest (too restricted access) campo cerrado vegetation. Related to this, it is important to note that the continued expansion of exotic grass species in Aguará Ñu could have potentially severe consequences for the study species, as its near-complete ground cover restricts access by roosting nightjars, and indeed any ground-roosting or foraging species (e.g. Tubelis & Cavalcanti 2000).

Nightjars also showed a preference for younger, and avoidance of older, campo cerrado habitats when selecting foraging sites, apparently as a result of differences in vegetation structure and abundance of their insect prey. Although this apparent predilection for younger habitats has been noted previously for the species (Lowen *et al.* 1997, Rodrigues *et al.* 1999), this is the first study to demonstrate it in a quantitative manner, and using data from radio-tagged individuals. The finding that foraging nightjars selectively avoided the most recently burnt vegetation, supported suggestions that birds benefited primarily from the abundant insect prey present in regrowing vegetation, rather than from changes in habitat structure and associated visibility (Rodrigues *et al.* 1999; Chapter 4).

In general, the factors that most determine the overall impact of a wildfire on the local flora and fauna, are its intensity, seasonal timing, duration, and the time since the last fire (Andersen *et al.* 1998, Mistry 1998, Silveira *et al.* 1999). Although timing and frequency are considered mainly in the context of their impact on intensity (i.e. through their effects on moisture content and fuel load, respectively), timing can be of considerable importance in its own right, particularly where the local biota displays seasonal patterns of growth and reproduction (Andersen *et al.* 1998). Until recently, there has been much resistance to active fire management in cerrado protected areas, where a 'no action' policy has generally prevailed (Pivello & Coutinho 1996). Nevertheless, the current situation of isolated fragments of protected habitat with limited ability for self-recovery, has encouraged active management (Pivello & Coutinho 1996), with prescribed burning increasingly being recognised as a vital management tool in the conservation of cerrado areas (Pivello & Norton 1996). A well-designed fire management system can address a number of key inter-related management objectives, including weed control, the reduction of tree density, and the maintenance of open areas and their typical species (Pivello & Norton 1996). However, its most important role is probably in reducing the frequency and extent of the exceptionally destructive wildfires that can otherwise occur as a result of fire exclusion programmes (Pivello & Norton 1996, Mistry 1998, Silveira *et al.* 1999).

Studies of their ranging behaviour showed that White-winged Nightjars were present at the study site throughout the year, and that they utilised home ranges averaging 28.0 ha in size, containing wet grassland and campo cerrado, but not forest, habitats (Chapter 4). Aguará Ñu protects approximately 3,800 ha of non-forested habitats, and thus a potential maximum population of

c. 150 White-winged Nightjars (assuming an average home range overlap of 20%; Chapter 4). However, a significant proportion of this area is dominated by dense palm cerrado, and unfortunately it still remains unclear whether the species utilises this habitat. Furthermore, searches for the species in the northern sector of Aguará Ñu have repeatedly failed to find it there, and it may be the case that this area is not suitable for the species. Nevertheless, assuming an area of just 1,000 ha of suitable habitat in southern Aguará Ñu, the protected population would probably total around 40 birds, six more than the tally of adult captures during this three-year study (Chapter 2). Overall, the upper and lower limits cited above coincide well with the estimate of 38-132 adults provided by Capper *et al.* (2000) on the basis of densities of displaying males.

Whilst the White-winged Nightjar is clearly not an abundant species, the findings of this study suggest that, potentially, it may not be as scarce as currently believed. The striking plumage of the male notwithstanding, various aspects of the species' behaviour – notably its avoidance of tracks and lack of far-carrying vocalisations (*cf.* sympatric species; e.g. Sick 1993) – mean that it is surprisingly easy to overlook. Nests and roost sites are extremely cryptic (Chapters 3 & 4), and the species' camouflaged plumage and reluctance to flush, make it very difficult to find by chance. Even individuals fitted with radio-transmitters proved frustratingly elusive on occasions, particularly when using areas of taller vegetation. In years without a spring burn, extensive areas of Aguará Ñu were dominated by the native grass *Loudetia flammida* (see Plate 4.2), the tall flowering stems of which reflected light from torches, and made nightjar eye-shine much more difficult to detect.

Bearing in mind these findings, it does not seem unreasonable to suggest that the White-winged Nightjar may exist undetected at other sites within the swath of Cerrado encompassing the modern and historical localities known for the species (Figure 1.1). One potential method of identifying new localities would be through the analysis of satellite (land cover) and physiographic data using GIS and computer modelling techniques (e.g. Avery & Haines-Young 1990, Tucker *et al.* 1997, Peterson 2001). Nevertheless, although the species may be more widespread than currently recognised, its ecology and habitat requirements clearly do render it sensitive to human disturbance (Chapter 4), and hence it may only persist in relatively undisturbed cerrado fragments. To allow for this, potential sites could be prioritised based on the similarity of their avifaunal inventories to the four modern localities (e.g. Cavalcanti 1999), with particular attention paid to the occurrence of species considered reliable 'indicators' of high-quality habitats (e.g. Parker *et al.* 1996). The Aguará Ñu bird list, for example, includes 13 bird species considered indicators of 'campo grasslands', and a further eight of 'low, seasonally wet grasslands', reflecting the comparatively undisturbed state of the site's grassland habitats.

Once target sites have been identified, the information obtained during this study on the White-winged Nightjar's activity patterns, breeding season and display behaviour (Chapters 3 & 4) could be used to devise census techniques that maximise the probability of detecting the species. Although the male display noise does not carry as far as the vocalisations of many other sympatric nightjars, it is still highly characteristic, and was used successfully to conduct an informal census of displaying males at Aguará Ñu in December 2000 (Pople 2001). Furthermore, the individual variation shown by males for temporal measures of the display noise (Chapter 3), hint at the potential for the use of sonographic analysis of display noises in future census work (e.g. McGregor & Byle 1992, Gilbert *et al.* 1994, Peake *et al.* 1998).

Overall, the topics outlined above can be distilled into seven key conservation recommendations:

- Protect and monitor key sites for the study species, such as the ridgelines in the southern Aguará Ñu where males establish display territories during the breeding season.
- Establish a fire management regime for Aguará Ñu, to control the timing and extent of burns, create and maintain a mosaic of vegetation of different ages, and prevent uncontrollable wildfires during the study species' breeding season.
- Document and monitor the spread of exotic grass species in Aguará Ñu, and investigate methods to control and eventually reverse their expansion.
- Describe the distribution and density of palm cerrado vegetation in Aguará Ñu, using aerial photos and satellite imagery, to facilitate future investigations into the use of this habitat by the study species, and improve estimates of the area of 'suitable' habitat available.
- Establish a monitoring programme of the local nightjar population, using the techniques tested successfully during this study, and investigating the potential use of individual variation in male display noise as a complementary census technique.
- Survey areas of non-protected cerrado habitats adjacent to Aguará Ñu, to assess their conservation value and potential for future purchase and protection.
- Utilise GIS techniques and satellite imagery to identify potential new localities for the study species, using avifaunal inventories – in particular the occurrence of 'indicator' species – to prioritise sites likely still to retain areas of undisturbed cerrado habitats.

GENERAL LIMITATIONS

Studies of rare and threatened species are, by their very nature, logistically and scientifically problematic (Caughley & Gunn 1996), and this thesis proved no exception. The nocturnal habits of the study species only served to complicate matters further, and inevitably some of the information presented in this thesis is somewhat descriptive in nature. Furthermore, throughout the study, sample sizes were frequently rather low, as a consequence of the small number of birds (particularly females) monitored or captured during the course of fieldwork, and occasionally this

must temper conclusions regarding the broader significance of some results. Nevertheless, great care was taken to ensure that sample sizes (e.g. of radio-tracking locations) were not artificially inflated by inappropriate sampling or pseudoreplication, and the assumptions and appropriateness of all statistical tests were checked thoroughly before carrying out tests of significance.

FINAL THOUGHT

The Dodo is lost forever, but we still have the opportunity to save species like the White-winged Nightjar from extinction. Its insect-like vocalisations and flatulent display noise might not be worthy of the description ‘song’, but they remain knowable to anyone willing to venture out into the cerrado night and listen. The sight of the ghostly male drifting in to his display arena, as the light from the sun fades and another night begins, is a special moment, and I would suggest that his subsequent dance routine more than makes up for any vocal inadequacies he may have. I only hope that the show will run for many moons more...

*“And hand in hand on the edge of the sand,
They danced by the light of the moon,
The moon,
The moon,
They danced by the light of the moon.”*

Edward Lear, *The Owl and the Pussycat* (1871)

Appendix I White scores, sexual plumage and size dimorphism, and ecological attributes of 82 species of Caprimulgidae.

Species	Wing white			Tail white			Throat white			Overall white			Wing length (mm)			Tail length (mm)			Ecological attributes			
	M	F	dm	M	F	dm	M	F	dm	M	F	dm	M	F	dm	M	F	dm	Hab	PC	Lat	
CHORDELINEAE																						
<i>Lurocalis semitorquatus</i>	0.0	0.0	-	1.0	0.0	-	2.0	2.0	2.0	1.0	0.0	-	0.00	178.2	176.4	-	79.8	78.5	-	4.25	B	4 N
<i>L. rufiventris</i>	0.0	0.0	-	0.9	1.5	-	2.0	2.0	2.0	0.9	1.5	-	0.00	206.3	208.0	-	83.7	90.0	-	4.25	?	7 S
<i>Chordeiles pusillus</i>	6.4	6.3	-	2.9	0.8	+	1.3	1.4	1.4	9.3	7.1	+	0.24	124.4	125.1	-	75.1	72.9	-	1.75	?	8 S
<i>C. vielliardi</i> *																						
<i>C. rupestris</i>	52.0	52.0	-	26.5	26.5	-	2.6	2.6	2.6	78.5	78.5	-	0.00	166.3	158.2	-	91.7	89.3	-	1.50	?	9 S
<i>C. acutipennis</i>	6.0	1.4	+	3.1	0.0	+	2.6	0.5	0.5	9.1	1.4	+	0.85	163.0	157.0	-	94.0	92.7	-	1.50	B	7 S
<i>C. minor</i>	8.4	6.0	+	3.6	0.0	+	1.8	0.4	0.4	12.0	6.0	+	0.50	198.0	196.5	-	110.9	112.0	-	2.00	B	48 N
<i>C. gundlachi</i>	8.7	4.2	+	3.8	0.0	+	2.8	1.0	1.0	12.5	4.2	+	0.67	170.2	168.7	-	93.9	95.5	-	1.50	?	21 N
<i>Nyctiprogne leucopyga</i>	0.0	0.0	-	3.4	3.4	-	0.8	0.8	0.8	3.4	3.4	-	0.00	133.1	127.6	-	85.7	85.0	-	2.67	?	7 N
<i>Podager nacunda</i>	17.0	10.3	+	11.1	0.0	+	2.4	1.6	1.6	28.1	10.3	+	0.63	255.1	237.6	-	119.0	111.8	-	1.50	?	20 S
CAPRIMULGINAE																						
<i>Nyctidromus albicollis</i>	10.5	2.5	+	18.3	1.2	+	2.4	1.6	1.6	28.8	3.7	+	0.87	154.3	152.3	-	144.4	136.7	-	4.00	B	9 S
<i>Phalaenoptilus nuttallii</i>	0.0	0.0	-	6.4	3.5	+	2.8	2.8	2.8	6.4	3.5	+	0.45	142.5	142.6	-	85.5	87.3	-	2.00	B	35 N
<i>Siphonorhis americanus</i> †																						
<i>S. brewsteri</i>	0.0	~	?	8.0	~	?	1.0			8.0	~	?		117.8	115.6	-	103.2	98.6	-	3.00	?	
<i>Nyctiphrynus mcleodii</i>	0.0	(0.0)	-	5.0	(5.0)	-	2.0			5.0	(5.0)	-	0.00	127.8	127.2	-	111.0	108.7	-	3.25	B	26 N
<i>N. yucatanicus</i>	(0.0)	0.0	-	(4.0)	4.0	-			3.0	(4.0)	4.0	-	0.00	111.9	111.2	-	103.2	101.5	-	3.00	?	18 N
<i>N. ocellatus</i>	0.0	0.0	-	5.5	3.1	+	2.0	2.0	2.0	5.5	3.1	+	0.44	128.6	123.9	-	116.5	111.5	-	4.50	?	18 S
<i>N. rosenbergi</i>	(0.0)	0.0	-	(5.0)	5.0	-			3.0	(5.0)	5.0	-	0.00	125.8	124.1	-	97.0	97.2	-	4.50	?	3 N
<i>Caprimulgus carolinensis</i>	0.0	0.0	-	9.4	0.0	+	0.4	0.2	0.2	9.4	0.0	+	1.00	213.4	208.1	-	142.7	136.5	-	4.00	?	36 N
<i>C. rufus</i>	0.0	0.0	-	6.1	0.0	+	0.0	0.0	0.0	6.1	0.0	+	1.00	170.1	167.4	-	116.8	112.4	-	3.75	?	2 N
<i>C. cubanensis</i>	(0.0)	(0.0)	-	(6.0)	(0.0)	+				(6.0)	(0.0)	+	1.00	181.0	178.7	-	133.1	129.2	-	3.00	B	22 N
<i>C. salvini</i>	(0.0)	(0.0)	-	(6.5)	(0.5)	+				(6.5)	(0.5)	+	0.92	172.6	169.3	-	130.5	123.5	-	3.00	?	22 N
<i>C. badius</i>	(0.0)	(0.0)	-	(8.0)	(0.0)	+				(8.0)	(0.0)	+	1.00	172.0	α	-	125.2	α	-	3.25	?	19 N
<i>C. sericocaudatus</i>	0.0	(0.0)	-	6.5	(0.0)	+			0.0	6.5	(0.0)	+	1.00	180.3	175.8	-	146.8	141.4	-	3.75	?	21 S
<i>C. ridgwayi</i>	0.0	0.0	-	6.5	0.0	+	1.0	1.0	1.0	6.5	0.0	+	1.00	157.5	160.3	-	118.2	119.3	-	3.00	?	23 N
<i>C. vociferus</i>	0.0	0.0	-	13.9	0.0	+	1.8	1.4	1.4	13.9	0.0	+	1.00	153.8	155.4	-	123.6	116.4	-	4.00	B	42 N

<i>C. poliocephalus</i>	3.5	0.8	+	15.5	4.8	+	0.2	0.4	19.0	5.6	+	0.71	154.0	150.0	-	119.0	111.5	-	4.25	B	9 N
<i>C. ruwenzorii</i>	3.2	0.9	+	8.0	3.6	+	0.8	0.3	11.2	4.5	+	0.60	157.8	157.0	-	116.4	112.5	-	3.25	?	3 S
<i>C. asiaticus</i>	4.6	3.8	-	6.9	4.9	+	1.4	1.2	11.5	8.7	+	0.24	147.1	145.6	-	106.0	104.0	-	2.75	B	16 N
<i>C. natalensis</i>	7.4	2.4	+	12.8	0.0	+	2.6	1.2	20.2	2.4	+	0.88	156.0	154.0	-	106.0	100.2	-	1.75	B	9 S
<i>C. inornatus</i>	5.0	0.0	+	8.6	0.0	+	0.0	0.0	13.6	0.0	+	1.00	158.5	156.0	-	124.0	116.5	-	2.25	?	16 N
<i>C. stellatus</i>	4.5	3.5	-	4.8	2.0	+	1.0	1.0	9.3	5.5	+	0.41	155.0	155.0	-	99.0	95.0	-	1.50	?	7 N
<i>C. affinis</i>	7.4	0.0	+	19.5	0.0	+	1.8	0.8	26.9	0.0	+	1.00	191.6	184.2	-	115.4	109.6	-	2.25	B	21 N
<i>C. tristigma</i>	1.9	1.4	-	5.7	0.0	+	0.6	0.8	7.6	1.4	+	0.82	180.6	178.8	-	122.2	117.4	-	1.75	B	6 N
<i>C. conreus</i>	0.0	0.0	-	3.0	0.0	+	2.5	2.0	3.0	0.0	+	1.00	169.8	168.5	-	104.0	103.3	-	5.00	?	0
<i>C. pulchellus</i>	(3.0)	(0.0)	+	(3.3)	(0.0)	+			(6.3)	(0.0)	+	1.00	153.5	152.0	-	97.6	96.5	-	5.00	?	3 S
<i>C. enarratus</i>	0.0	0.0	-	1.3	2.0	-	0.0	0.0	1.3	2.0	-	0.00	145.2	148.2	-	106.8	109.2	-	5.00	B	19 S
<i>C. batesi</i>	2.6	0.0	+	3.6	0.0	+	1.0	0.8	6.3	0.0	+	1.00	191.0	192.0	-	152.5	152.0	-	4.75	?	0
<i>C. climacurus</i>	8.8	2.8	+	4.3	0.0	+	1.7	1.8	13.1	2.8	+	0.79	145.0	143.0	-	243.0	175.0	+	3.00	?	8 N
<i>C. clarus</i>	12.8	5.8	+	4.7	0.0	+	1.6	1.4	17.5	5.8	+	0.67	148.0	145.0	-	131.0	118.0	+	2.50	?	1 N
<i>C. fossii</i>	7.7	2.9	+	3.9	0.0	+	1.6	1.0	11.6	2.9	+	0.75	163.2	159.0	-	126.2	117.1	-	2.00	B	15 S
<i>C. solala</i> *																					
<i>Macrodipteryx longipennis</i>	0.0	0.0	-	0.0	0.0	-	0.0	0.0	0.0	0.0	-	0.00	485.8	168.5	+	110.0	108.0	-	2.50	F	10 N
<i>M. vexillarius</i>	29.5	0.0	+	0.0	0.0	-	1.4	0.4	29.5	0.0	+	1.00	626.5	188.0	+	143.0	127.0	+	3.00	F	15 S
<i>Hydropsalis climacocera</i>	9.6	0.5	+	23.3	0.0	+	1.2	0.0	32.9	0.5	+	0.98	157.2	154.0	-	150.4	129.3	+	3.83	?	8 S
<i>H. brasiliiana</i>	0.0	0.0	-	2.2	0.0	+	0.0	0.0	2.2	0.0	+	1.00	170.2	164.0	-	275.6	136.0	+	2.75	?	11 S
<i>Uropsalis segmentata</i>	0.0	0.0	-	0.0	0.0	-	0.0	0.0	0.0	0.0	-	0.00	169.8	165.0	-	467.0	119.0	+	3.50	?	2 N
<i>U. lyra</i>	0.0	0.0	-	0.0	0.0	-	0.0	0.0	0.0	0.0	-	0.00	174.4	182.5	-	666.0	142.5	+	4.00	?	2 N
<i>Macropsalis creagra</i>	0.0	0.0	-	7.9	0.0	+	0.0	0.0	7.9	0.0	+	1.00	229.8	194.0	+	608.0	176.0	+	4.00	?	25 S
<i>Eleothreptus anomalus</i>	3.5	0.0	+	2.0	0.0	+	0.0	0.0	5.5	0.0	+	1.00	130.7	132.0	-	72.5	80.3	-	2.00	?	26 S

* = known only from single adult museum specimen.

† = not reliably recorded since 1860 and presumed extinct (BirdLife International 2000).

‡ = white 'scalloping' on trailing edge of primaries difficult to quantify.

~ = insufficient information available to score plumage of female.

α = mean data for female morphometrics not available, but no evidence for sexual size dimorphism based on ranges in Cleere (1998).

Scores in parentheses indicate those derived from photos or detailed descriptions available in the literature, rather than direct inspection of museum specimens.

Hab = score for structural density of breeding habitats.

PC = parental care of offspring; B = both sexes confirmed to care; F = female only cares; ? = nature of parental care uncertain.

Lat = latitudinal midpoint of breeding range (°).

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